THE TEMPORAL AND SPATIAL PROPERTIES OF LARGE-FIELD MOTION-DETECTION NEURONS IN LOBULA PLATE OF THE FLY

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DECLARATION

I declare that all the original work presented in this thesis is my own except for Chapter 5, part of which was written by Prof. G.A. Horridge, when we published a joint paper ons the H1 neuron (Proc. R. Soc. Lond. 1990).

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ABSTRACT

This thesis reveals several aspects of the electrophysiological properties of the H1 and V2 neurons (the large-field motion-detectors) in the lobula plate of the blowfly Lucilia cuprina, by investigating the responses of about 170 cells to a bar or a grating movement with a continued motion, or a brief jump, or a sinusoidally modulated velocity, in experiments lasting many hours on each cell.

The temporal properties of the H1 and V2 neurons are studied mainly in Chapter 3, involving the transient response characteristics, the afterimage effects of the stimulus and their influences on the responses of the neurons, the temporal integration, and the temporal similarity of the H1 and V2 neurons.

Then, attention is drawn to the spatial properties of the neurons (Chapter 4), where the possible spatial structure of the elementary motion detectors (EMDs), the response spatial interaction, the lateral interactions between the EMDs, and the possibility that two kinds of motion detection channels are involved.

Finally, the measurements of the LFMDs are examined in Chapter 5. The results demonstrate that the H1 neuron mainly measures velocity contrast in the steady state, irrespective of mean velocity, acceleration, velocity modulation frequency, spatial frequency, contrast frequency, and intensity contrast.

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CHAPTER ONE

GENERAL INTRODUCTION

1-1. Functions of motion detection systems.

Motion detection is a basic function of the visual system, serving many aspects of vision, for example, to define object boundaries relative to a distant background (Nakayama and Loomis 1974), to pick up the three-dimensional arrangement of the environment (Hildreth and Koch 1987), to judge relative depth (Prazdny 1980), or to estimate time to contact (Lee 1980, Wagner 1982). Study of the motion detection system of insects provides a practical way to understand how the information is processed in a relatively simple biological system with some hope of success, to help solve, for example, human vision research and robot vision. Over the past decades, many efforts have been made on various insect species with different experimental methods. Motion-sensitive neurons have already been found in different levels of the nervous system of insects, for example, those discovered early (Burtt & Catton 1954; Horridge et al. 1965; Collett and Blest 1966; Bishop and Keehn 1966), to those recently found in the bee (Kaiser 1970 and DeVoe et al. 1982; Hertel and Maronde 1987), the fly (Hausen 1981; Eckert 1982; Hengstenberg et al. 1982; Umeda and Tateda 1985; Egelhaaf 1985), the locust (Kien 1974; Osorio 1986) and the moth (Rind 1983). Reviews of directionally selective motion neurons in the optic lobes of insects have been made by some authors (for example Wehner 1981). Although no actual synaptic mechanisms of directional motion detectors have been revealed, many artificial models and algorithms have been proposed and tested (O'Shea and Rowell 1977; Ullman 1981; Buchner 1984; Rind 1987).

1-2. Structures of motion detectors.

There is strong evidence that the insect motion detection system consists of thousands of elementary motion detector subunits (EMD's), all of similar morphological and physiological properties, which respond in parallel to the movement of whatever is in their visual field and send the information to a large-field collector neuron called a large-field motion-detection neuron (LFMDN). The theoretical structure of the EMD proposed over the past 25 years involves the fundamental idea that, for correct indication of the direction of movement, a multiplication or subtraction is carried out between the signals from each adjacent pair of visual receptors.

The correlation model.

One of the well known models for the EMD based on the idea of multiplication is the correlation model (Hassenstein and Reichardt 1953, 1956), and several variants of it (Thorson 1966; Kirschfeld 1972;Buchner 1976; Mastebroek et al. 1980;van Santen and Sperling 1985). In this model, the motion is the autocorrelation of a pattern with itself displaced in time and space. One receptor picks up a modulation from the pattern; the adjacent receptor receives the same modulation a moment later. Therefore if the first modulation is delayed and then multiplied continuously with the second where they converge, the output reaches a maximum when the temporal repeat period of the pattern matches the delay irrespective of the spatial frequency. The model has successfully explained the time-averaged optomotor response of walking or flying flies to continuously moving periodic and nonperiodic stimulus patterns (see reviews by Reichardt 1961, 1969, 1987; Gotz 1965, 1972; Poggio and Reichardt 1976; Buchner 1984), and even been used to modeling directionally selective motion detection in the visual system of vertebrates (Schouten 1967; Foster 1971; van Doorn and

Koenderink 1976; Bulthoff and Gotz 1979; van Santen and Sperling 1984; Wilson 1985; Emerson et al.1987). The problems with this model are that many models make the same prediction, and in visual systems the stimulus is convolved with the fields of neurons, not the stimulus with itself.

The gradient model.

Quite a different model (called the gradient model), recently proposed to measure the velocity of moving objects (Limb and Murphy 1975; Fennema and Thompson 1979), operates according to the formula: the angular velocity equals the rate of change of the receptor response with time, divided by the rate of change of the response with angle:

$$v = d\phi/dt = dI/dt \div dI/d\phi$$

Here, v is velocity (°/s),

ø is angular distance (degrees),

I is illuminance.

This computation was suggested as a model for motion detection in vertebrate cortical cells (Marr and Ullman 1981).

Experiments on the fly (McCann 1974, Zaagman, Mastebroek & Kuiper 1978) indicate that directional motion detection is based on correlation-like interaction rather than on a gradient-computing mechanism. The above works do not contain the ideas that other systems may be used or that direction of motion may be detected by one mechanism, and angular velocity measured by another. However, recent work by Horridge & Marcelja (1990), with responses to bars which jump and reverse contrast, suggest that multiplication, and therefore

autocorrelation, do not occur. This has been followed by similar work on random patterns (Horridge & Marcelja 1991).

The visual signals processed in parallel by these EMDs then makes a summation on high level motion detectors (MDs). Elsewhere there must be additional higher level visual functions such as figure-background discriminations, detection of parallax and estimations of depth, by other neurons. One of the difficulties of analysis of nervous systems is that they contain arrays of neurons in parallel, converging upon similar arrays, so that you never know what is happening in other neurons that are not being recorded simultaneously.

1-3. The problems we faced in this thesis.

What simple features should we measure to clarify the operation of such higher level mechanisms? Which details are significant in recording their activity? How can we elucidate the optimization processes and compromises that have evolved in a parallel processing array to enable the neurons to function so effectively? Clearly, when only one neuron can be observed at one time the temporal and spatial properties of neurons become significant. A second difficulty is how to analyze a system which is apparently part of a feedback circuit when we have only one of the neurons which we believe interacts with its own inputs. Again, the temporal relations of the excitation at different points in the circuit become significant.

Questions that can be addressed now are: (a) what aspects of the motion information do the EMDs pick up from the environment; (b) what are the temporal and spatial characteristics of this processing; (c) how many types of EMD exist in the motion detection system; and (d) do all EMDs have the same temporal and spatial properties. So far little attention has been paid to these

important details of motion detection, but, even appropriate methods of investigation have not been forthcoming. Therefore we addressed these problems by quantitatively analyzing the responses of the motion-sensitive neurons of the fly lobula plate with different motion stimulations. The main reason for choosing these neurons is that they are well-known in morphology (Hausen 1981), they can be consistently isolated and recorded extracellularly for a long time, they sum the responses of many EMDs in parallel, and their responses apparently reflect the properties of many similar EMD channels feeding into one neural network.

1-4. The H1 and V2 neurons - the large-field motion-detectors.

The neurons recorded in the fly lobula plate include wide-field motion-sensitive directionally-selective neurons responding to flow field components for all possible degrees of freedom of the fly's motion (Hausen 1981). They were divided into two main groups according to their directional selectivity, i.e., (H), sensitive to horizontal motion and (V), sensitive to vertical motion. The majority of my recordings were made from two already-identified neurons known as the H1 and V2 neurons (Hausen 1976; Eckert 1980; Maddess & Laughlin 1985). The H1 neuron is readily found and separated from other neurons; it is located at the posterior part of the lobula plate and crosses the brain to the opposite optic lobe, a feature which effectively separates it from other motion-sensitive neurons and also leaves undisturbed the stimulated eye and optic lobe. The H1 neuron responds to regressive motion of any contrasting stimulus across the eye i.e. from posterior to anterior at the side of the eye (called the prefered direction), and is inhibited by forward motion of the eye (null direction). This neuron can be recorded for many hours with an extracellular electrode. Its receptive field covers the entire ipsilateral eye, and is believed to receive a retinotopic array of inputs either directly from the medulla, or via the outer lobula (e.g. Strausfeldt

1984); i.e. it has numerous inputs in parallel from the whole field of the eye; it has a projection to the contralateral optic lobe where it presumably interacts with other visual information. Thus it is probably a fourth or fifth order interneuron.

1-5. Previous work on H1 and V2.

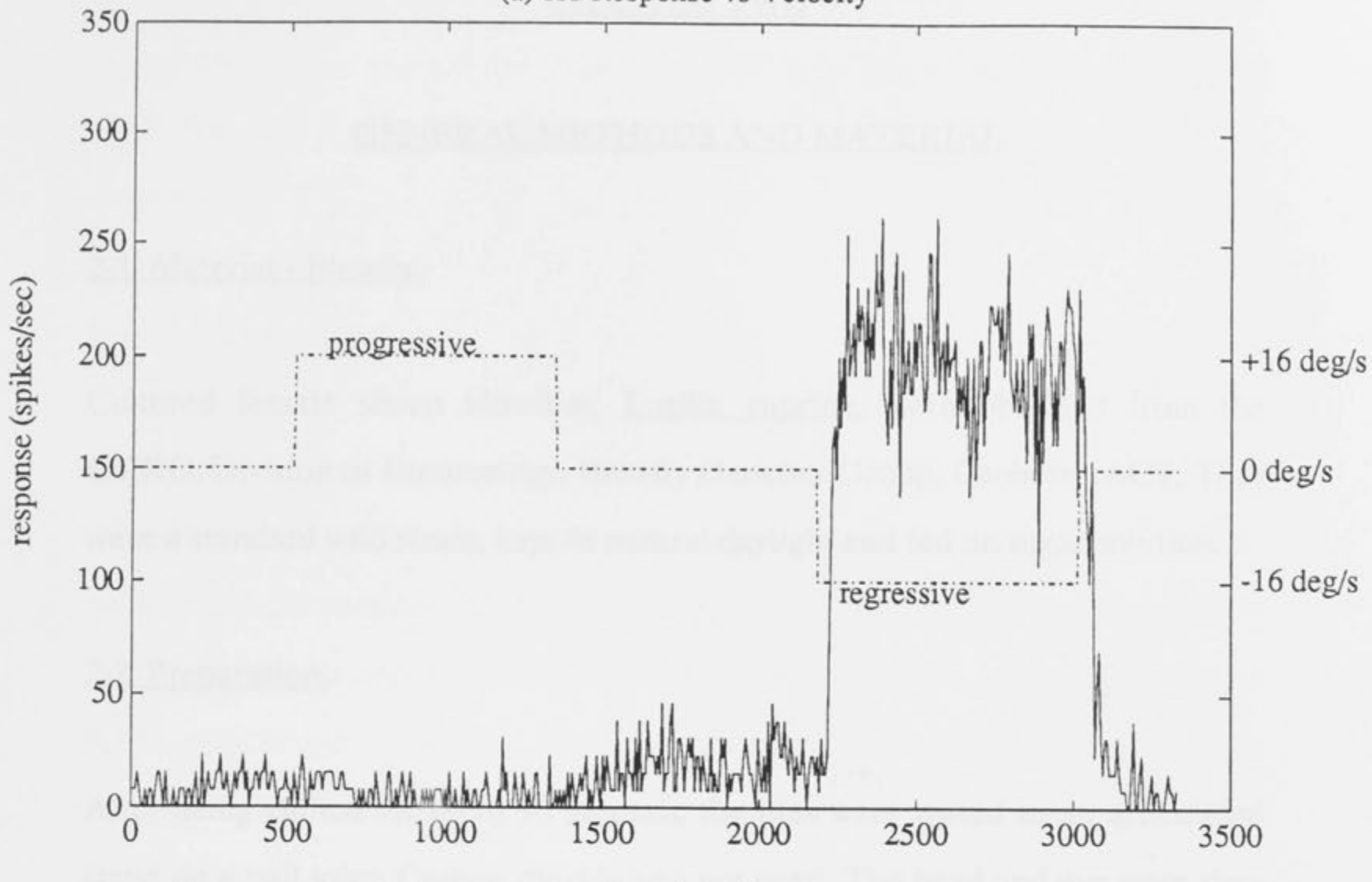
Most of the introductory work on the H1 neuron originated from the research of Masterbroek (1974), Dvorak & Bishop (1975), and Hausen (1976). In the early days the H1 neuron was just one of the directionally-selective movement receptors with a wide contralateral field. Subsequently, quartitative work was done by the group at Groningen, Netherlands. Attention was first directed to the statistical properties of the spike train (Zaagman 1977). Apart from a small excess of short intervals between them, the spikes are Poisson-distributed in time. The distribution of inter-spike intervals is exponential, with variance proportional to the mean interval (if bursts of spike are arbitrarily excluded), a feature which can be explained for any neurons as preventing false cross-correlations between different neurons with a background discharge.

The V2 neuron is of particular interest to us here, because only a few works deal with it (Hausen 1976 a & b; 1981). By making a comparison with the H1 neuron it provides us with a practical chance to reveal whether or not all motion detectors consist of the same or similar EMDs. So the experiments are mainly exploring the characteristics of the V2 neuron, which is a heterolateral cell connecting both sides of the lobula plate; its preferred direction is ipsilateral downward motion and, a weak response also can be elicited by regressive motion.

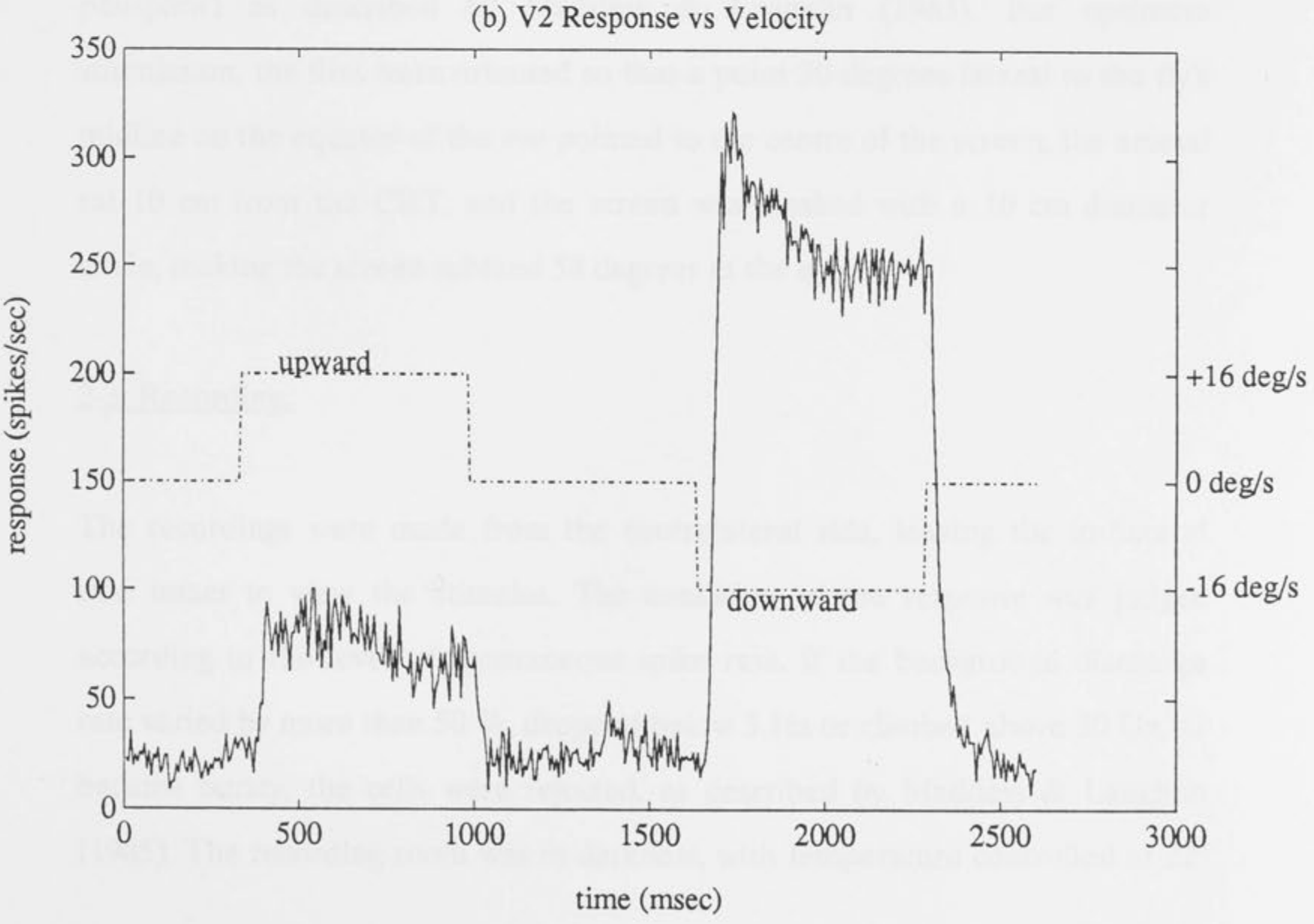
The typical response of the V2 neuron is shown in Fig.1-I. The stimulus was a sine wave grating of spatial frequency 0.14 cyc/deg, and intensity contrast 0.3, moving either upward or downward with a speed of 16.6 deg/sec for 0.83 seconds, with a stationary phase of 0.83 seconds between the motion phases. The response was measured as the firing frequency of the neuron, averaged over 100 repetitions of the stimulus. The response to motion in the preferred direction consists of an initial transient peak followed by a steady maintained component.

Figure 1-I. Responses of the H1 and V2 neurons to movement of a sinusoidal grating of wavelength 6.6° and intensity contrast 0.3 with a speed of 16 °/s. The grating was manipulated in the following sequence for 100 trials at intervals of about 3.3 seconds in (a) or 2.4 seconds in (b). First the pattern remained stationary on the CRT screen for 832 ms (a) or 600 ms (b), then moved through the field of view in the null direction for the same period as in phase one, then remained stationary, and finally moved in the preferred direction for a period of (a) 832 ms or (b) 600 ms. Motion in the preferred direction generated a large response, but to motion in the opposite direction the spike firing frequency of H1 was inhibited (a) and V2 gave a relative weak response (b).

(a) H1 Response vs Velocity



(b) V2 Response vs Velocity



CHAPTER TWO

GENERAL METHODS AND MATERIAL

2-1. Material - Blowfly.

Cultured female sheep blowflies, Lucilia cuprina, were obtained from the CSIRO, Division of Entomology, Blowfly Genetics Group, Canberra ACT. They were a standard wild strain, kept in natural daylight and fed on sugar solution.

2-2. Preparation.

After being chilled for 60 to 90 seconds, the flies were waxed to an articulated stand on a ball joint. Carbon dioxide was not used. The head and eye were then aligned to the centre of the screen of a cathode ray tube (type 609 with P31 phosphor) as described by Maddess & Laughlin (1985). For optimum stimulation, the flies were oriented so that a point 30 degrees lateral to the fly's midline on the equator of the eye pointed to the centre of the screen, the animal sat 10 cm from the CRT, and the screen was masked with a 10 cm diameter circle, making the screen subtend 58 degrees at the eye.

2-3. Recording.

The recordings were made from the contralateral side, leaving the ipsilateral side intact to view the stimulus. The condition of the response was judged according to the level of spontaneous spike rate. If the background discharge rate varied by more than 50 %, dropped below 5 Hz or climbed above 30 Hz, or became bursty, the cells were rejected, as described by Maddess & Laughlin (1985). The recording room was in darkness, with temperature controlled at 22°

± 2°. All flies were light-adapted to their position in front of the screen, and illuminated at an average brightness of 7 cd/m*m for at least 20 min before recording, and first experiments were repeated at the end of a run to ensure consistency.

2-4. Visual stimulus.

Visual stimuli were generated by a computer (PDP 11/03) with a frame rate of 160 Hz and vertical resolution of 1024 lines, corresponding to about 0.05° for each line in visual angle, which was similar to that used by Dvorak et al (1980). Stimuli were sine-wave or square-wave gratings, or a single bar with a rectangular intensity profile. Stimulus parameters under experimental control were mean velocity, acceleration, duration of continuous movement, and jump distance. Spikes were amplified by a Grass Preamplifier P16 with a high-pass filter of 100 Hz corner frequency, passed though a Schmitt trigger, collected by the on-line computer and displayed as post-stimulus time histograms with average numbers of spikes in bins 6.5 ms wide. All results presented here were obtained by averaging between 50 and 100 trials.

CHAPTER THREE

TEMPORAL PROPERTIES OF THE LFMDS

THE RESPONSES OF H1 AND V2 TO GRATING STIMULI

Abstract

In this part of the experiments, the H1 and V2 neurons were stimulated by sine and square wave gratings with a constant contrast of 0.3 and various moving speeds and spatial frequencies, to mainly test the temporal and spatial properties of the input channels - the presumedly elementary motion detectors (EMDs). The results indicate that both H1 and V2 neurons, in functional terms, possess EMD inputs with similar spatial and temporal structures. The EMDs are found to measure mainly the displacement of a stimulus which has been integrated in spatial and temporal domains in the transient response state, with a spatial discrimination of about 0.13°, linear integration distance of up to 0.4° and integration time about 13 ms to 60 ms, depending on the speeds. The EMDs may be able to discriminate motion velocities up to about 64 °/s in the transient state, since below this velocity the neurons can produce transient responses with different initial firing acceleration according to the various speeds. Another method, makes use of the afterimage effects which provides an influence of the stimulus spatial structure temporally on the EMD's responses. The H1 and V2 neurons apparently assemble the motion signals from similarly structured EMDs which are sensitive in the same way to the contrast between previous and present light illuminance. Actually, there is no significant difference in the responses to the stimuli of sine-wave and square-wave gratings when testing afterimage effects, suggesting that the EMDs may simply count the number of passing edges. The direction-selectivity of the neurons is temporally lost when affected by the afterimage, but can be restored in response to a continuous movement which can efficiently eliminate the afterimage.

3-1. Introduction.

A major part of the function of fly's neuron system is the detection of local motion in the complex visual environment of the animal. This filtering process is performed mainly by the medulla for small fields, and for large fields is already complete at the lobula plate, typically by the horizontal and vertical large-field motion-detection neurons. A knowledge of the properties of the H1 and V2 neurons, therefore, provides an important indication of the function of the motion detection system as a whole. Several characteristics of H1 and V2 are of particular interest in this chapter, notably temporal filtering, i.e, the response adaptation, the afterimage effects and the temporal integration of the response.

When responding to a sudden motion, the H1 and V2 neurons fire normally in two phases - a initial transient part which mainly reflects stimulus strength, and a subsequent steady state in which the decline of response is determined eventually from the time of stimulus onset. So in the following experiments, the investigation was concentrated mainly on the properties of the transient state by measuring the response strength and time constants versus the stimulus velocity and displacement, as well as the stimulus spatial frequency.

The afterimage effect is an interesting feature of the motion detectors in their transient response state and probably represents the properties of the EMDs. If the neuron is exposed to a stationary periodic pattern for a while, then the response of the neuron oscillates in time when the pattern is moved. This oscillation in response amplitude was related to an afterimage of the periodical pattern by Maddess (1986). No doubt it must reflect some intrinsic properties of the motion detectors, so that studying the afterimage becomes a practical way to examine the spatial and temporal characteristics of the motion detector in the transient response state.

The H1 and V2 neurons are one of a group of big giant cells in the lobula plate of the flies (Hausen 1981), with a receptive field which covers much of one eye. In functional terms they receive visual information from the large number of parallel distributed elementary motion detectors (EMD's). The responses of H1 and V2 are generally thought to reflect an integration of the responses of the EMD's in the temporal and spatial domains (Srinivasan 1983), and are probably influenced by some kinds of lateral interaction and feed-back influences. So, at this stage it is time to determine the relationship between the response strength and the summation of stimulus displacements; to measure the integration time as well as the influence of stimulus velocity on it; and finally to examine the possibility of lateral interaction and feed-back loops in the fly's motion detection system.

To satisfy our goals of this stage, square and sine-wave gratings are the most appropriate stimulus patterns, simply because a large part of the movements of a natural visual environment can be simulated and simplified by these pattern's motions, and because many response phenomena such as adaptation, afterimage and integration can be efficiently studied with these stimuli.

3-2. Methods.

The experiments were carried out on wild-type female sheep blowflies, Lucilia cuprina, which were obtained from lab colonies and were 7-10 days post emergence. The unanaesthetized fly was immobilized with wax on a movable ball joint stand, with the head bent forward; and then the right eye was positioned towards the centre of the screen of a cathode ray tube (type 609 with p31 phosphor) with the fly's midline 30° lateral to the screen. A small hole was cut in the back of the left side of the head and the air sacs overlying the recording site were carefully removed so that a small portion of the posterior

surface of the optic lobe was clearly exposed. A drop of saline was added into the exposed region as needed. A silver wire serving as the reference electrode penetrated this saline pool and was waxed. This procedure is the same as that of Dvorak, Srinivasan and French (1979).

Square- and sine-wave gratings were produced on the computer driven CRT display, whose spectral output was well matched to the spectral sensitivity of the fly's photoreceptors (Dvorak et al, 1979). The refresh time of the pattern was 6.5 ms and each frame contained 1024-lines. The gratings, with different spatial frequencies, mean luminances and luminance contrasts, could either be held stationary, or be made to drift in either horizontal or vertical directions at various velocities.

Extracellular responses were recorded with tungsten microelectrodes (Hubel, 1957) after the method of Merrill and Ainsworth (1972), amplified, filtered with 100 Hz corner frequency and displayed in the standard manner. After a single cell was isolated and its preferred direction noted, normally two kinds of stimulus procedures were followed - one with prior-motion and the other without prior-motion. The responses were collected and stored by the on-line computer (PDP-11-3), which counted the number of spikes per picture refresh synchronized to the time of a velocity change, which was same as previously done in this laboratory (Maddess & Laughlin 1985). All the results presented here were obtained by averaging between 77 and 100 trials.

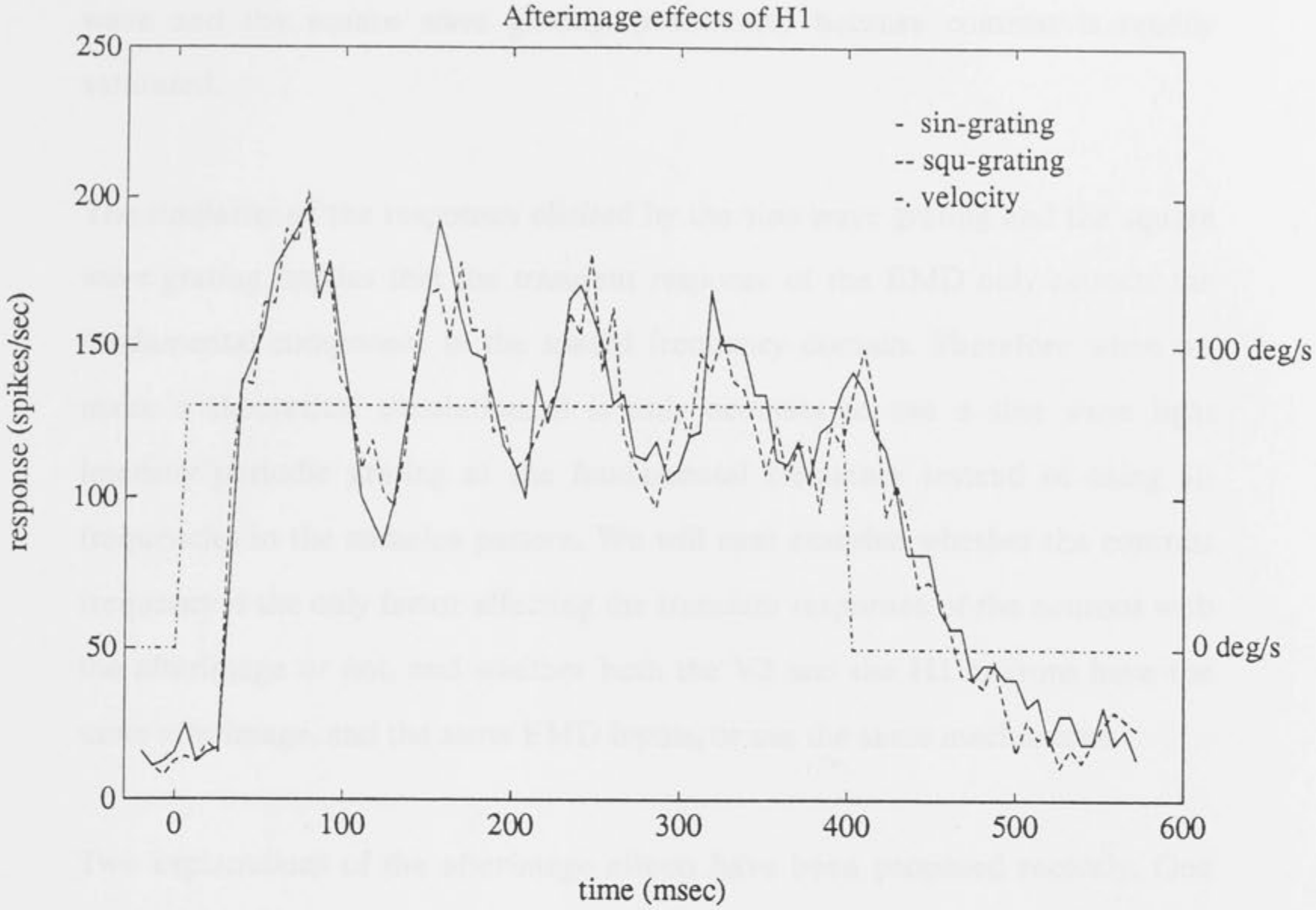
3-3. Experimental results.

The results describe the responses of about 40 neurons recorded extracellularly from the lobula plate of the fly. These neurons fit into the class called wide-field directionally-selective motion-detecting neurons (DSMD) by Hausen (1976,1981), which were responding to a motion stimulus by increasing the spike firing rate in the preferred direction, and decreasing the spike frequency (the H1 neuron) or weakly firing (the V2 neuron) in the null direction. In this part we are dealing mainly with the transient response, from which the properties of the EMDs are inferred for both H1 and V2 cells in terms of their temporal and spatial parameters. Later the interaction between EMDs will be explored. Finally we expect to reveal some properties and characteristics of the directionally-selective motion-sensitive neurons.

3-3-1. The afterimage effect of the LFMDs.

The afterimage is easily demonstrated quite consistently on a H1 neuron (figure 3-1). The stimulus pattern was a grating with a spatial frequency 0.15 deg/cyc, intensity contrast 0.3, and possessed a sine (a) or square (b) wave intensity profile. The pattern first remained stationary on the screen for two seconds to adapt the neuron, then moved at a constant speed of 80 deg/s for about 390 ms to elicit the response. The responses, averaged 100 times, show a clear sinusoidally-modulated oscillation, locked to the phase difference between the moving grating and its initial position. The peak amplitude of the response appeared at 180° phase separation from the initial position, and the trough at 360°. The two response curves, generated by the sine and square wave gratings respectively, also coincided very well (figure 3-1). No significant difference was observed either in the response wave shapes or the modulation between the sine

Figure 3-1. An example of afterimage effects of the H1 neuron. The stimulus was a vertical sine or square wave grating of spatial frequency 0.15 cyc/deg and contrast 0.3. The afterimage was generated in the following sequence. The grating first remained stationary on the screen for 2 seconds to adapt the neuron, then moved in the preferred direction at a constant speed of 80 °/s for about 400 ms to reveal the afterimage. The neuron shows an oscillation of the spike discharge. There is no significant difference in the response modulation to the sine wave and the square wave, suggesting that the transient response of the EMD extracts only the fundamental component of the pattern.


Afterimage effects of H1
- sin-grating
-- squ-grating
-. velocity
response (spikes/sec)
250
200
150
100
50
0
100 deg/s
0 deg/s
0
100
200
300
400
500
600
time (msec)

wave and the square wave grating, presumably because contrast is readily saturated.

The similarity of the responses elicited by the sine wave grating and the square wave grating implies that the transient response of the EMD only extracts the fundamental component in the spatial frequency domain. Therefore when we make a theoretical simulation, it is only necessay to use a sine wave light intensity periodic grating at the fundamental frequency instead of using all frequencies in the stimulus pattern. We will next examine whether the contrast frequency is the only factor affecting the transient responses of the neurons with the afterimage or not, and whether both the V2 and the H1 neurons have the same afterimage, and the same EMD inputs, or use the same mechanisms.

Two explanations of the afterimage effects have been proposed recently. One idea is that the afterimage is produced by local changes of the EMD sensitivity (Maddess 1986). It was suggested that the stationary or slowly moving periodic pattern alters the relative sensitivity of the eye regions, or neurons projecting from these regions, and that the alteration persists for several seconds. Another idea introduced by Egelhaaf (1988) was that the afterimage effect was introduced by a low pass filter acting on the output of the photoreceptors. Actually there is no fundamental difference between those ideas, the low pass filter can be considered as one form of sensitivity change. As expected by any theory, the mathematical simulation of Egelhaaf's scheme (with the correlation model) has been successful in predicting that the oscillation frequency of the fly HS neuron, when a sine wave intensity grating was suddenly changed from stationary to moving, was determined by the temporal frequency of stimulation (Egelhaaf 1988), but it was not able to explain the facts that the decay time constant of the afterimage effects was also a function of the temporal frequency

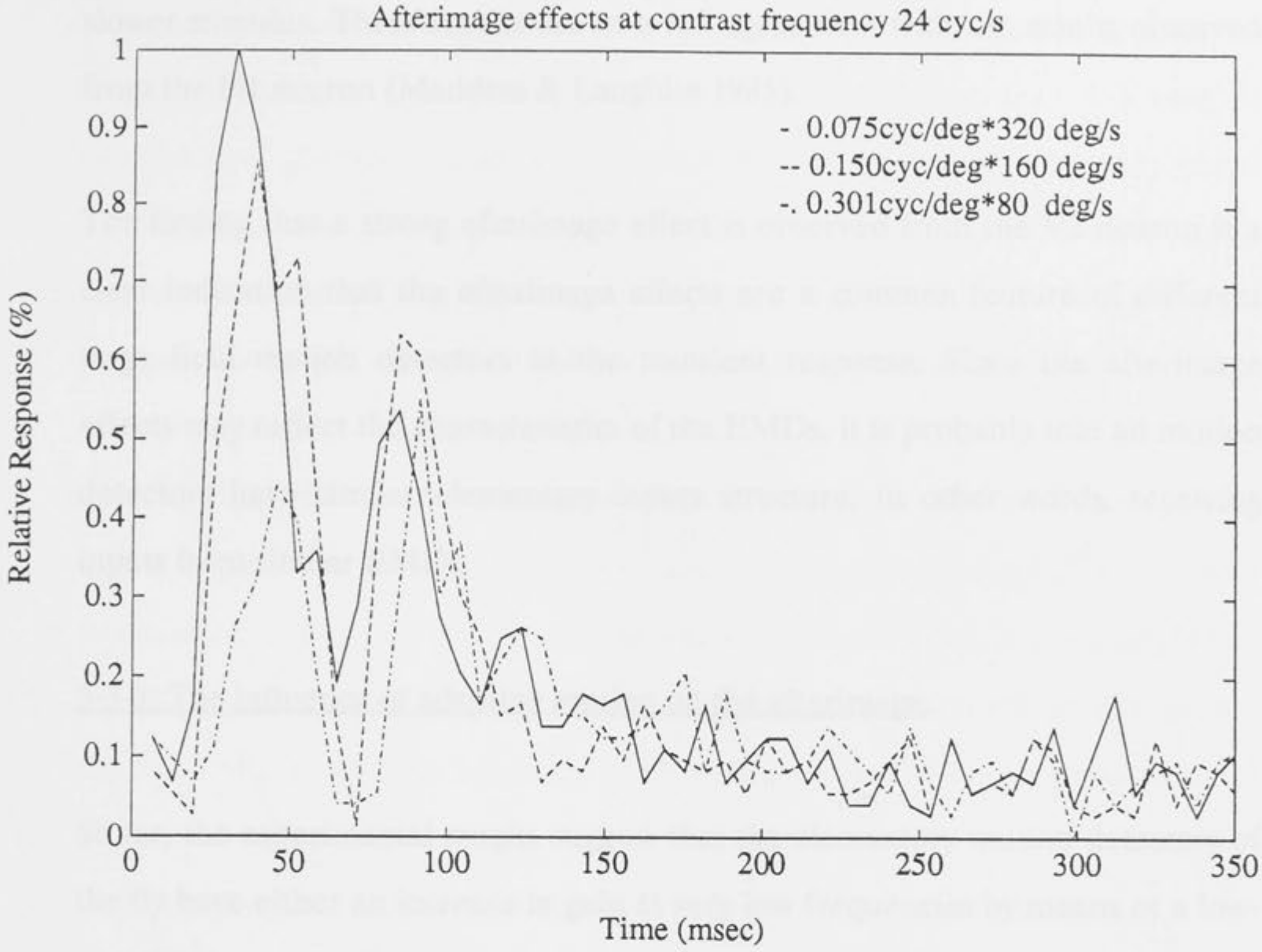
of the moving grating and that the amplitude of response was influenced by prior-motion.

3-3-2. The influence of contrast frequency on afterimage effects.

Next, we examine the effect of stimulus contrast frequency on the response with the afterimage by recording the responses to a constant contrast frequency with three different velocity-spatial frequency combinations. These experiments were on a V2 neuron, which preferred the stimulus direction downward with the receptive field over the whole ipsilateral side. A square wave grating with illumination intensity contrast of 0.3 was used at this stage as a test pattern, with spatial frequencies separately at (a) 0.075 cyc/deg, (b) 0.15 cyc/deg and (c) 0.30 cyc/deg, correspondingly, to keep the same contrast frequency of 22.4 cyc/s for all stimulation, the motion speeds were (a) 320 deg/s, (b) 160 deg/s and (c) 80 deg/s. The procedure was similar to that in the experiment of 3-3-1, but the duration of the grating movement was shortened to 65 ms so that the effects of motion adaptation to the neurons could be reduced to a minimum. Responses were averaged 100 times.

When we examine the responses versus the contrast frequency, an independence of the response strength on the stimulus contrast frequency becomes clear, though the frequency of the responses modulation is equal to the contrast frequency of the test stimulus in all three cases (figure 3-2). The amplitude of the response modulation was greater when the stimulus pattern was of lower spatial frequency and moved faster, especially at the first peak. The amplitude of the response to 320 deg/s with spatial frequency of 0.075 cyc/deg was twice as high as to 80 deg/s at the spatial frequency of 0.28 cyc/deg. Also the phase of the modulated response generated by the faster stimulus precedes that due to the

Figure 3-2. Demonstration that the contrast frequency determines the frequency of the response modulation. The experiment was done on a V2 neuron with square wave grating of intensity contrast 0.3. The spatial frequencies of the grating were chosen separately at 0.075, 0.15 and 0.3 cyc/deg. To keep the same contrast frequency of 24 cyc/s, the motion speeds were correspondingly 320 °/s, 160 °/s and 80 °/s. The stimulus procedure was similar to that in Fig. 3-1, but the duration of the grating movement was 65 ms. The oscillation frequency depends on the contrast frequency of the test stimulus, irrespective of velocity and spatial frequency, with the strongest response and the shortest time to peak in response to the most rapid motion.


Afterimage effects at contrast frequency 24 cyc/s
- 0.075cyc/deg*320 deg/s
-- 0.150cyc/deg*160 deg/s
-. 0.301cyc/deg*80 deg/s
Relative Response (%)
Time (msec)
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
0
50
100
150
200
250
300
350

slower stimulus. These results are in a full agreement with the results observed from the H1 neuron (Maddess & Laughlin 1985).

The finding that a strong afterimage effect is observed from the V2 neuron is a clear indication that the afterimage effects are a common feature of different large field motion detectors in the transient response. Since the afterimage effects may reflect the characteristics of the EMDs, it is probable that all motion detectors have similar elementary inputs structure, in other words, receiving inputs from similar EMDs.

3-3-3. The influence of adapting motion on the afterimage.

So far, the experimental results suggest that the elementary motion detectors of the fly have either an increase in gain at very low frequencies by means of a low-pass filter or a feedback mechanism with the same effect. Let us now consider the effect of feedback. It is known that the noise in the inputs will have a bigger negative influence on the accuracy of the output, and a narrower temporal frequency response range in the absence of feedback than with feed back. A motion-perception system obviously prefers to produce an accurate response with a wider response-frequency range. Consequently we look for signs of a feedback loop by studying the influences of the history of stimulation on the responses of the motion detectors.

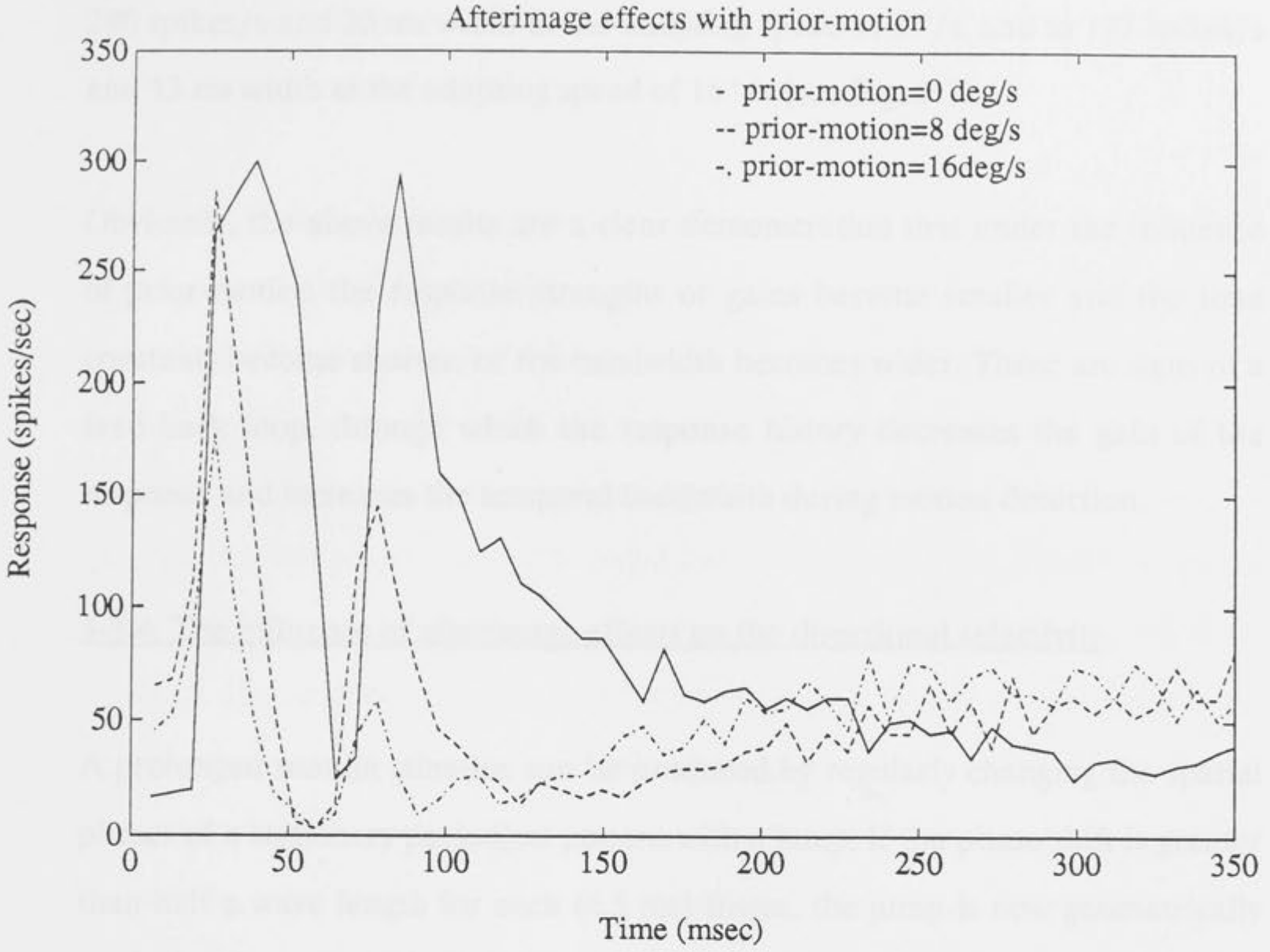
The presence of a feed back loop was sought on the basis that tests on the phasic response without prior-motion stimulation (or without an adapting motion stimulus) can be considered functionally as open-loop experiments, because at the moment of giving the test stimulus there is no signal feed back to influence the response of the motion detector. With the prior-motion stimulus we can search for the effect of a closed-loop, because the previous responses will

influence the present responses of the motion detecting system. If there is negative feed-back we expect that the modulation of responses will become weaker, and the decay time of the response will become shorter with prior-motion stimulation. This is because theory predicts that if the feed-back loop is closed, the gain of the system will become smaller and the range of the frequency response will become wider compared to the open loop case.

The experiments were done by measuring the afterimages in the V2 neuron with different adapting speeds. A square wave grating of contrast 0.3 and spatial frequency 0.15 cyc/deg was first moved at speeds of (a) 0 deg/s, (b) 8 deg/s and (c) 16 deg/s for one second as an adapting stimulus to generate an afterimage, then abruptly changed to a test speed of 160 deg/s above the adapting speed to reveal the effects of the afterimage. A brief (65 ms) test stimulus was used to avoid adapting the motion detector with prolonged motion (Maddess 1986).

The responses oscillated at the contrast frequency of the stimulation in all cases (figure 3-3), which is how we define the afterimage effects. But due to the short duration of the stimulation only two peaks of response amplitude were observed, corresponding to only two cycles of the stimulus grating being moved across each sampling point on the eye during the test stimulus. As the speeds of adapting motion increased, two effects were seen: The amplitude of the response modulation became weaker and the decline of the afterimage effects was faster. If we define the ratio of the amplitude of the second peak to the first one as a measure of the modulation strength, the ratios reduced from 0.97 when the adapting speed was 0 °/s, to 0.5 at adapting speed of 8 °/s, and to 0.3 at an adapting speed of 16 °/s. Secondly, with increasing adapting speed, responses became faster, the amplitude of each peak became smaller and the widths at 50% of peak height became narrower. For example, the first peak, which was about 300 spikes/s and 35 ms width at the adapting speed of 0 °/s, decreased to

Figure 3-3. The influence of prior-motion on an afterimage. The responses were recorded from a V2 neuron to a square wave grating of contrast 0.3 and wavelength 6.6 degrees. The grating was first moved at speeds of 0 °/s, 8 °/s and 16 °/s for one second as an adapting stimulus to generate an afterimage, then suddenly changed to a probe speed of 160 °/s for 65 ms to elicit a response which exposed the afterimage effects. The responses all oscillated in the same frequency, which indicates that the afterimage effects are formed by moving pattern as with the stationary pattern. This phenomena was found for the H1 neuron by Maddess (1986), and is similar in the H1 and V2 neurons. But, with the speed of prior-motion increasing, the amplitude of the response modulation became weaker, and the decline of the afterimage effects was faster, in other words the time constant became shorter. These features suggest a feedback loop which decreases the gain of the response and shortens the time constant or increases the temporal bandwidth.


Afterimage effects with prior-motion
- prior-motion=0 deg/s
-- prior-motion=8 deg/s
-. prior-motion=16deg/s
Response (spikes/sec)
Time (msec)
0
50
100
150
200
250
300
350

280 spikes/s and 20 ms width at the adapting speed of 8 °/s, and to 177 spikes/s and 13 ms width at the adapting speed of 16 °/s (see Fig. 3-3).

Obviously, the above results are a clear demonstration that under the influence of prior-motion the response strengths or gains become smaller and the time constants become shorter, or the bandwidth becomes wider. These are signs of a feed back loop, through which the response history decreases the gain of the response and increases the temporal bandwidth during motion detection.

3-3-4. The influence of afterimage effects on the directional selectivity.

A prolonged motion stimulus can be produced by regularly changing the spatial phases of a stationary periodical pattern with a jump. If the phase shift is greater than half a wave length for each (6.5 ms) frame, the jump is now geometrically equivalent to a move in the opposite direction. Thus the directionally selective motion detector will then give a weak response (for example the V2 neuron) or a negative one (for example the H1 neuron). In fact, the responses are necessarily a maximum when the phase jump in each frame is one quarter of a wave length and zero when it is half a wavelength. Because the stationary period and the size of the jump can be varied independently, this is a useful stimulus to explore the influence of the afterimage on the directional selectivity of the neurons.

The experiments were carried out on the H1 neuron, recorded when affected by the afterimage or after abolition of the afterimage. The afterimage was generated as described above in 3-3-1. Abolition of the afterimage was achieved by moving the stimulus pattern at a speed of 16 deg/sec for about 830 ms, which is believed to be fast and long enough to eliminate the afterimage. Then followed test speeds of 80 deg/s, 160 deg/s, 320 deg/s and 480 deg/s, relative to the adapting speed, with a duration of 65 ms. The stimulus pattern was a square

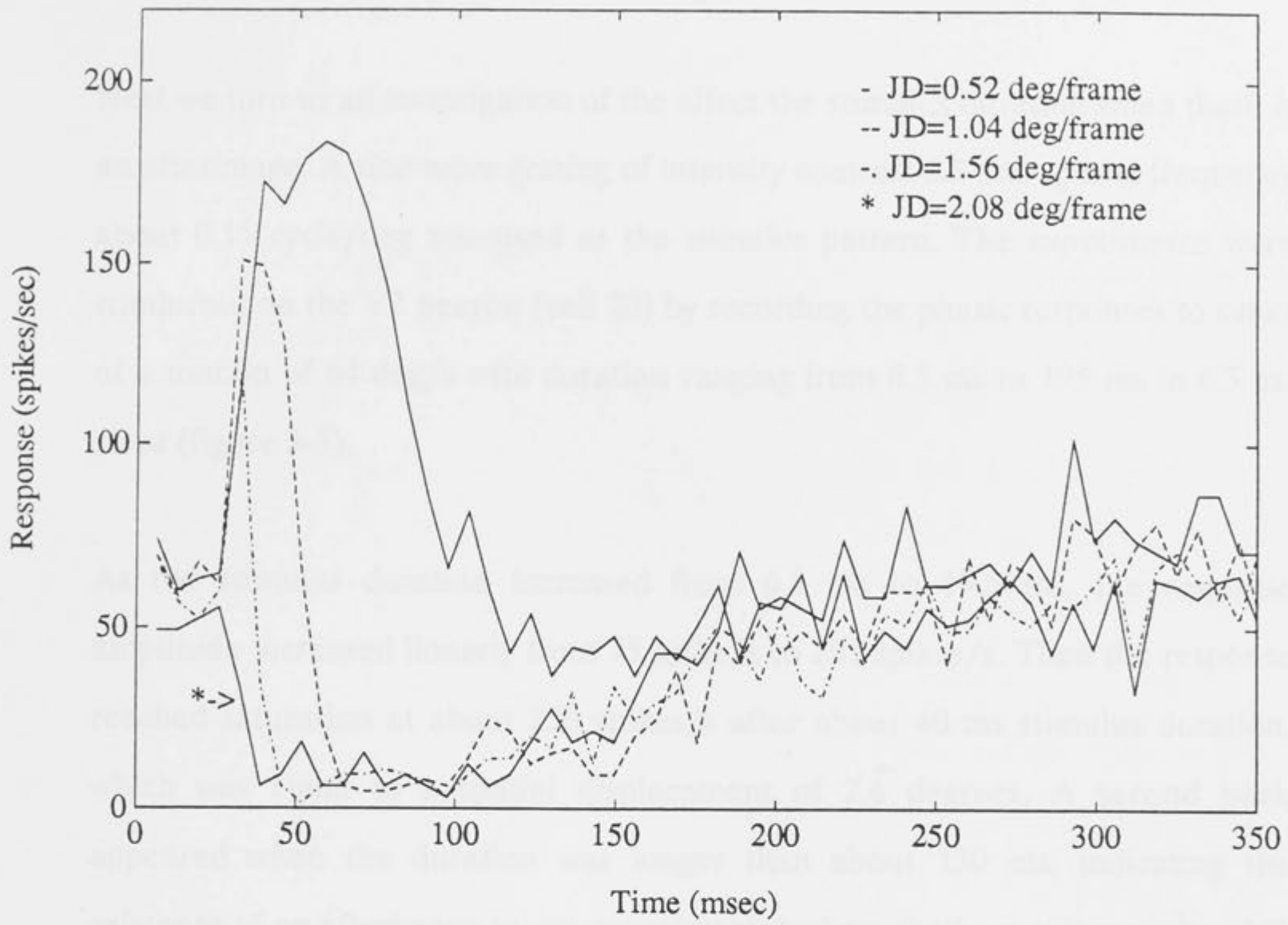
wave grating with spatial frequency of 0.15 cyc/deg and contrast of 0.3. The responses were averaged 100 times.

After abolishing the afterimage a strong directional-sensitivity was obtained. There was a weakened response when the distance jumped between each frame was more than one quarter of a wave length (figure 3-4a for cell 7). As the testing speed increased from 80 deg/s to 320 deg/s, the amplitude declined from 184 spikes/s to 120 spikes/s, which was only twice the background firing rate; the duration at 50% of peak also shortened from 65 ms to 6.5 ms. Finally, when the averaged speed of the jumping pattern reached 480 deg/s, which was when the stimulus displacement in each frame time was close to half a wave length, the positive response phase has totally disappeared. A negative phase was already observed when the speed was as low as 160 deg/s. No oscillation in the response amplitude was observed, showing that the afterimage affect had gone. Undoubtedly, the above findings are a clear indication that without the afterimage effect the neuron has a strong directional sensitivity, giving a predictable response to a jumping stimulus under experimental conditions.

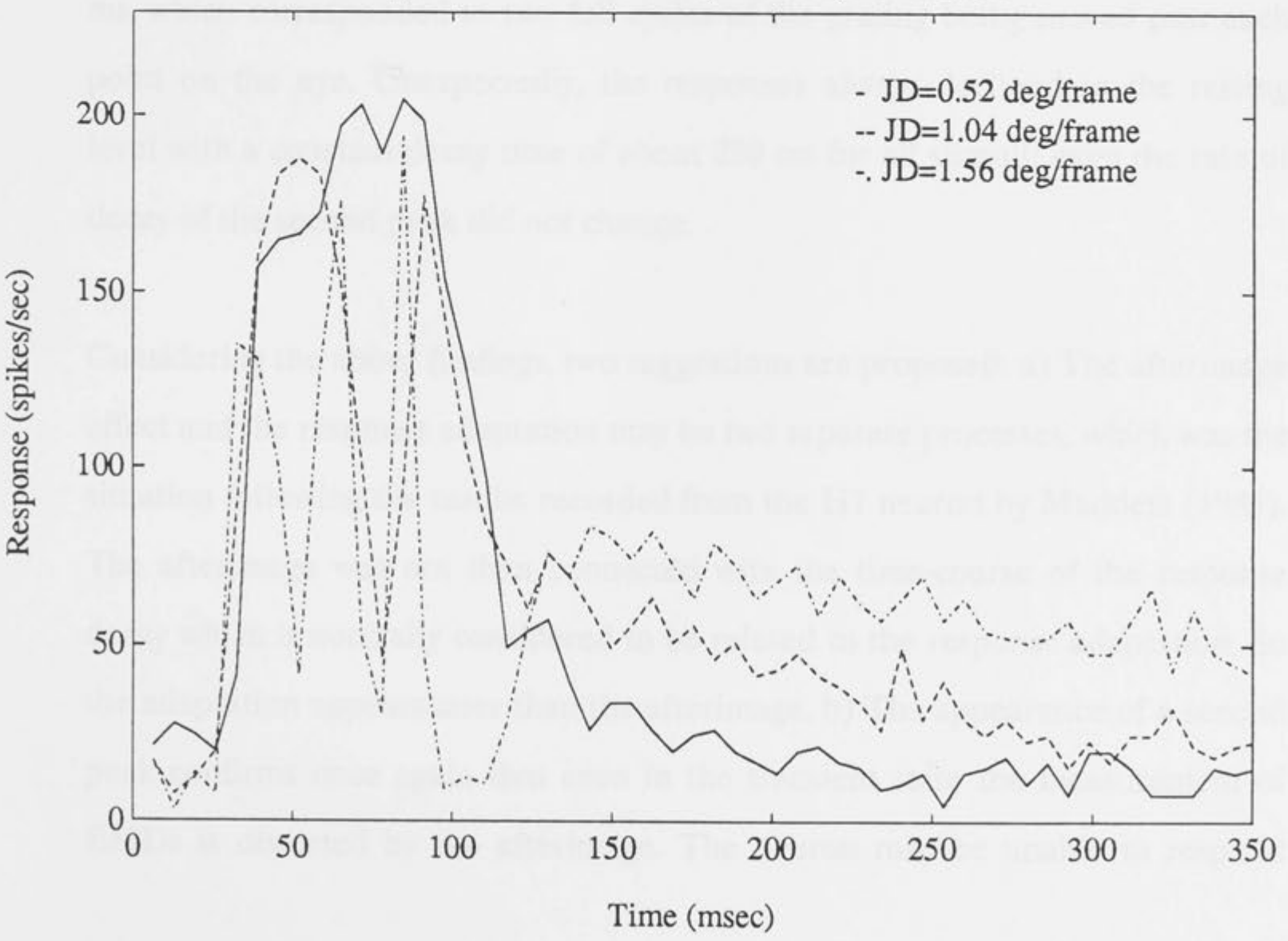
In contrast, directional sensitivity is lost when the cell is affected by an afterimage. This has been demonstrated by recording in the same conditions except for the afterimage (cell 6 in figure 3-4b). The afterimage is revealed by the number of peaks, according to how many cycles of the stimulus was passed at each point on the eye, but the point is that all responses had a similar amplitude. This is in strong contrast to the previous result, where only one peak appeared following a negative phase, and the peak's amplitude decreased with increasing jump distances (Fig. 3-4a).

Figure 3-4. The influence of the afterimage on the directional selectivity of the H1 neuron. The responses were recorded to a square wave grating of wavelength 6.6° and contrast 0.3, (a) without or (b) with afterimage effects. The afterimage was generated in the same way as in figure 3-2, the afterimage was eliminated in (a) by first moving the stimulus pattern at a speed of 16 °/s for about 830 ms. The test speeds were 80 °/s, 160 °/s, 320 °/s and 480 °/s, correspondingly about 0.52 °/frame, 1.04 °/frame, 1.56 °/frame and 2.08 °/frame, with the test duration 65 ms and the frame time 6.5 ms. After abolishing the afterimage, the neuron produced weaker responses as the distance in each frame moved closer to one quarter of the wave length, and even only a negative response when the distance moved at each frame was larger than one quarter of the wave length, which indicates that the neuron exhibits a strong directional selectivity as described in section 3-3-4. (b) With afterimage effects, however, the neuron gave responses with similar modulation strength at each test stimulus, indicating a loss of directional selectivity with the afterimage effect.

(a) Directional selectivity with prior-motion at 16 deg/s



(b) Directional selectivity without prior-motion



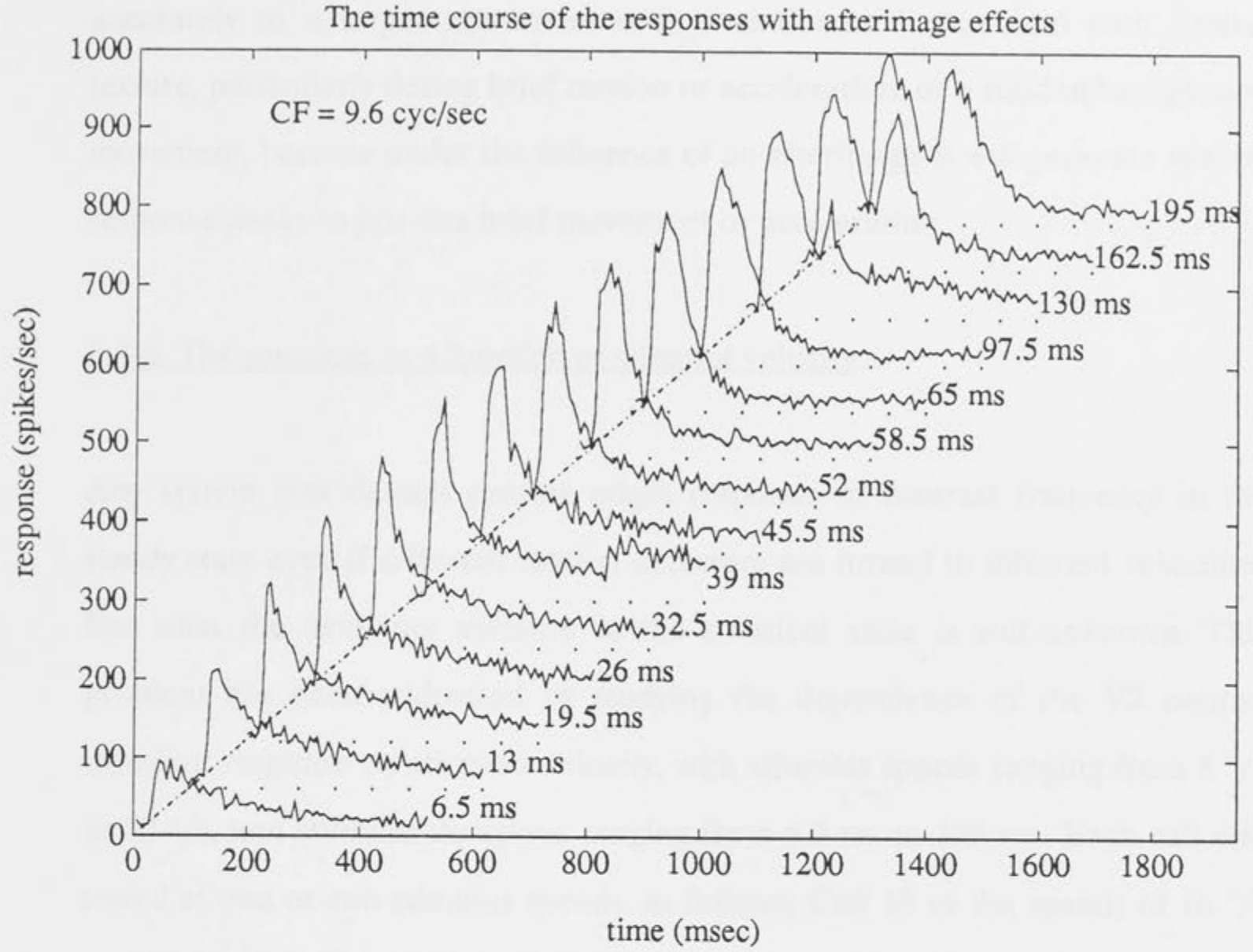
3-3-5. The phasic response as a function of stimulus duration.

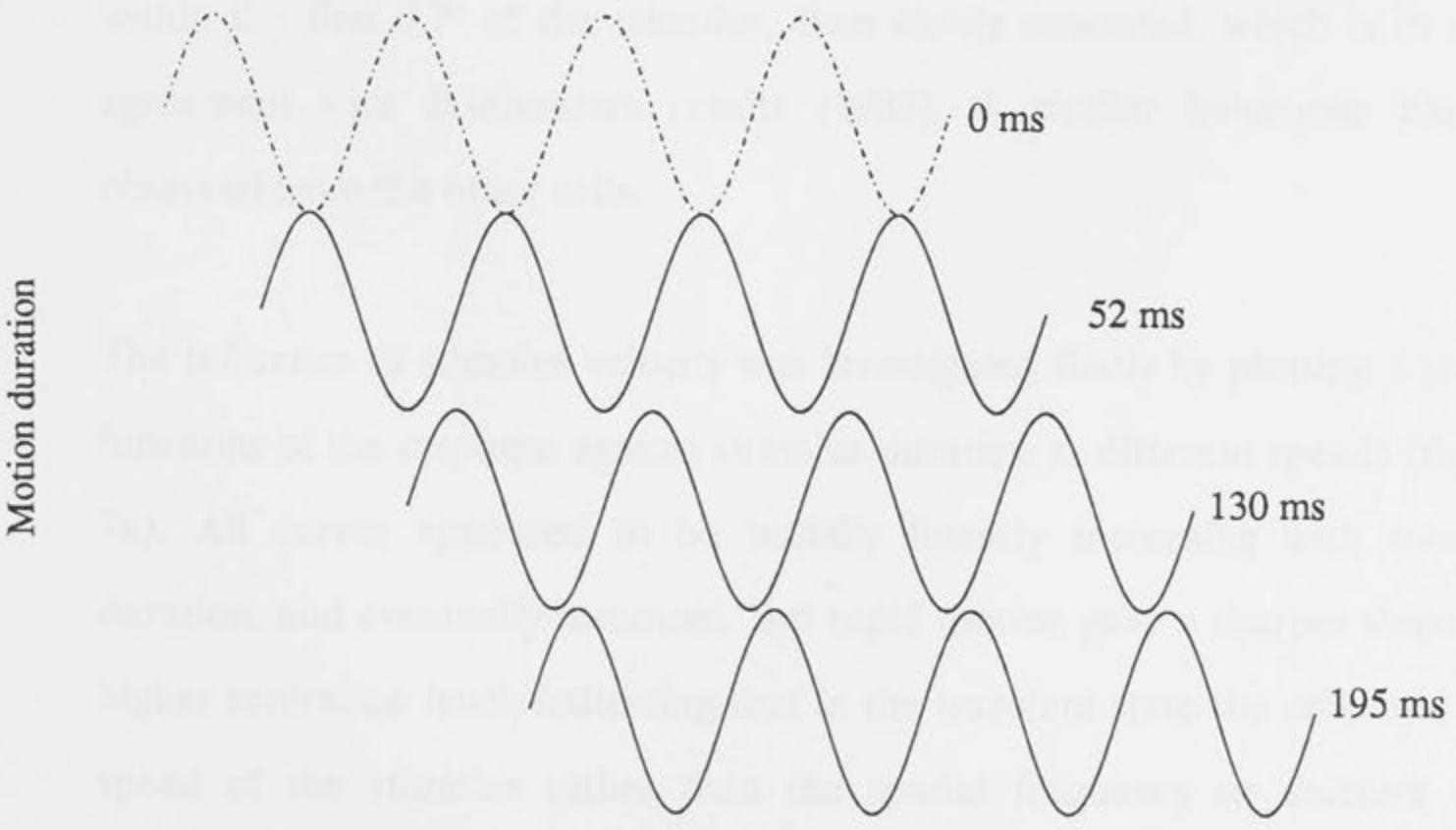
Next we turn to an investigation of the effect the stimulus duration when there is an afterimage. A sine wave grating of intensity contrast 0.3 and spatial frequency about 0.15 cycle/deg was used as the stimulus pattern. The experiments were conducted on the V2 neuron (cell 20) by recording the phasic responses to onset of a motion of 64 deg/s with duration ranging from 6.5 ms to 195 ms in 6.5 ms steps (figure 3-5).

As the stimulus duration increased from 6.5 ms to 19.5 ms, the response amplitude increased linearly from 75 spike/s to 201 spikes/s. Then the response reached saturation at about 250 spikes/s after about 40 ms stimulus duration, which was equal to a spatial displacement of 2.6 degrees. A second peak appeared when the duration was longer than about 130 ms, indicating the existence of an afterimage in our experiment; and reached a maximum after 163 ms stimulation. Finally it appeared to be completed at a stimulus duration of 195 ms, which corresponded to two full cycles of the grating being moved past each point on the eye. Unexpectedly, the responses always declined to the resting level with a constant decay time of about 250 ms for all stimuli; even the rate of decay of the second peak did not change.

Considering the above findings, two suggestions are proposed: a) The afterimage effect and the response adaptation may be two separate processes, which was the situation following the results recorded from the H1 neuron by Maddess (1985). The afterimage was not then connected with the time-course of the response decay which is normally considered to be related to the response adaptation. So the adaptation appears later than the afterimage. b) The appearance of a second peak confirms once again that even in the transient state the measurement of EMDs is distorted by the afterimage. The neuron may be unable to respond

Figure 3-5. The time course of the responses with afterimage effects. The stimulus pattern was a sine wave grating of contrast 0.3 and wavelength 6.6°. The pattern first remained stationary for 2 seconds, then moved at a speed 64 °/s with a duration ranging from 6.5 ms to 195 ms in 6.5 ms steps. The procedure was repeated 100 times. As the duration increased from 6.5 ms to 52 ms, the response increased from 75 spikes/sec to a maximum at about 270 spike/sec. A 52 ms motion means that a half wavelength of the pattern moved past the eye, giving the strongest contrast between the moving grating and the previous stationary grating, so that the biggest response was recorded. When the grating moved for 130 ms, about one and quarter of wavelength was passed across the previous stationary grating, so that the second peak appeared. When moving for 195 ms, nearly two cycles passed, so that the width of the second peak was equal to the width of the first one. Below is an illustration of the moving grating passing the stationary grating.





A sine wave grating moving at speed 64 deg/sec

accurately to a target movement over a stationary background with similar texture, particularly during brief motion or acceleration, or a sudden background movement, because under the influence of an afterimage it will generate several response peaks to just one brief movement or acceleration.

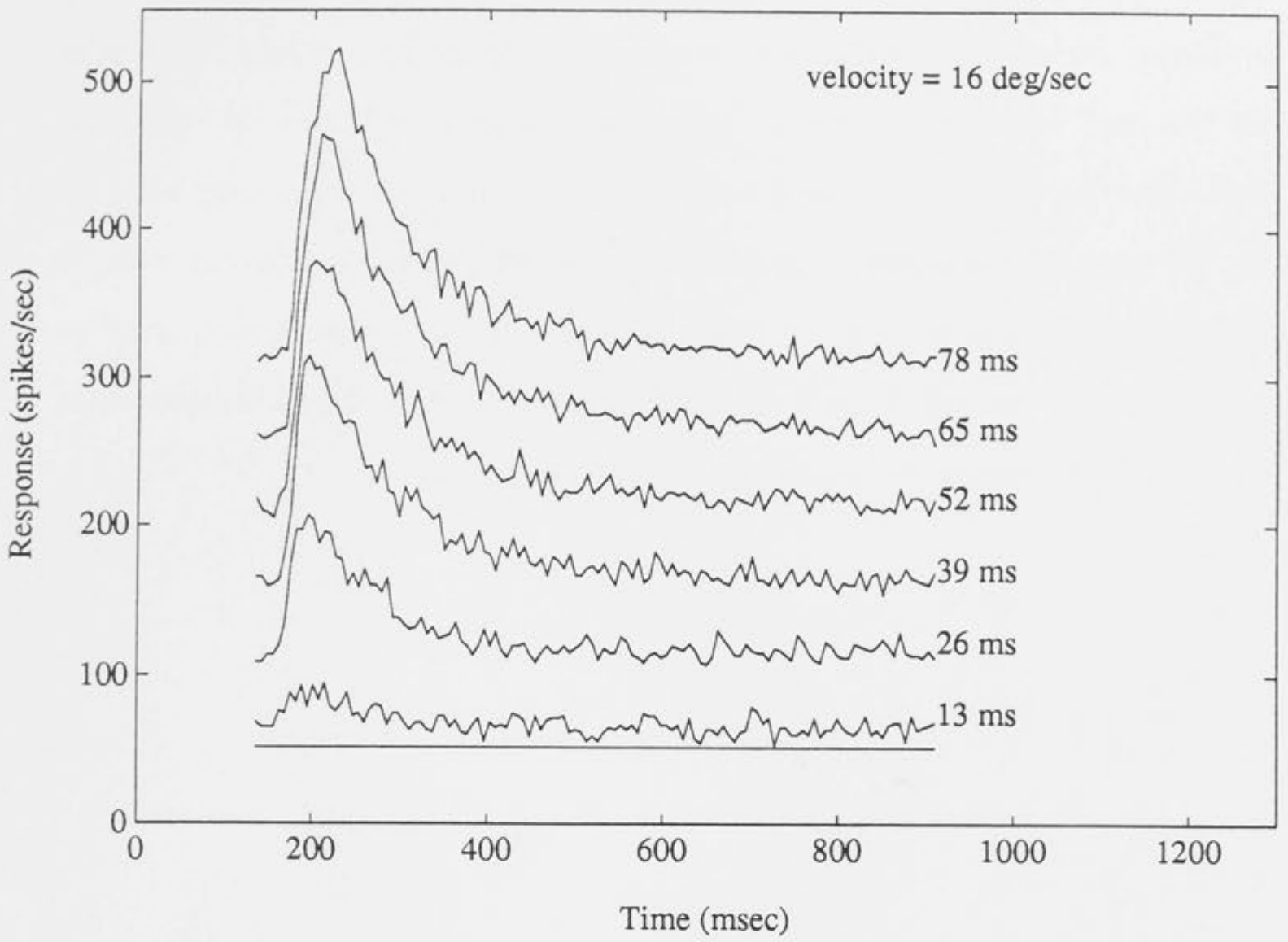
3-3-6. The response as a function of stimulus velocity.

Any system that detects passing edges responds to contrast frequency in the steady state even if different motion detectors are turned to different velocities. But what the detectors measure in the transient state is still unknown. This problem has been addressed by studying the dependence of the V2 neuron transient response on stimulus velocity, with stimulus speeds ranging from 8 °/s to 80 °/s, and stimulus durations ranging from 6.5 ms to 195 ms. Each cell was tested at one or two stimulus speeds, as follows: Cell 15 to the speeds of 16 °/s and 32 °/s; cell 16 to 8 °/s and 48 °/s; cell 20 to 64 °/s and cell 21 to 80 °/s. An example, recorded from cell 15 to a motion of 16 °/s with duration ranging from 13 ms to 78 ms, is given in Figure 3-6. The response increased almost linearly within the first 0.7° of the stimulus, then slowly saturated, which is in a good agreement with Srinivasan's results (1983). A similar behaviour has been observed from the other cells.

The influence of stimulus velocity was investigated firstly by plotting a series of functions of the response against stimulus duration at different speeds (figure 3-7a). All curves appeared to be initially linearly increasing with increasing duration, and eventually saturated. But rapid motion gave a sharper slope and a higher saturation level, indicating that in the transient state the cells may signal speed of the stimulus rather than the spatial frequency or stucture of the stimulus, because the curves should have similar slope if the cells mainly signal spatial frequency.

Figure 3-6. (a) and (b). Responses of a V2 neuron to the onset of a moving sine wave grating at speeds (a) 16 °/s and (b) 32 °/s with different durations. Generally speaking, as the duration increased, the response increased nearly linearly at first, then saturated. However, comparing (a) and (b), it is seen that the response is to the distance moved, especially during the first 0.7°. For example, the responses to the stimulus durations of 6.5 ms, 13 ms and 19 ms at speed 32 °/s appear to be similar in strength to the responses to 13 ms, 25 ms and 39 ms at speed 16 °/s. However, the initial slope of the response to a fast motion is more sharper than to a slow motion.

(a) Response vs Stimulus duration at speed 16 deg/s



(b) Response vs Stimulus duration at speed 32 deg/s

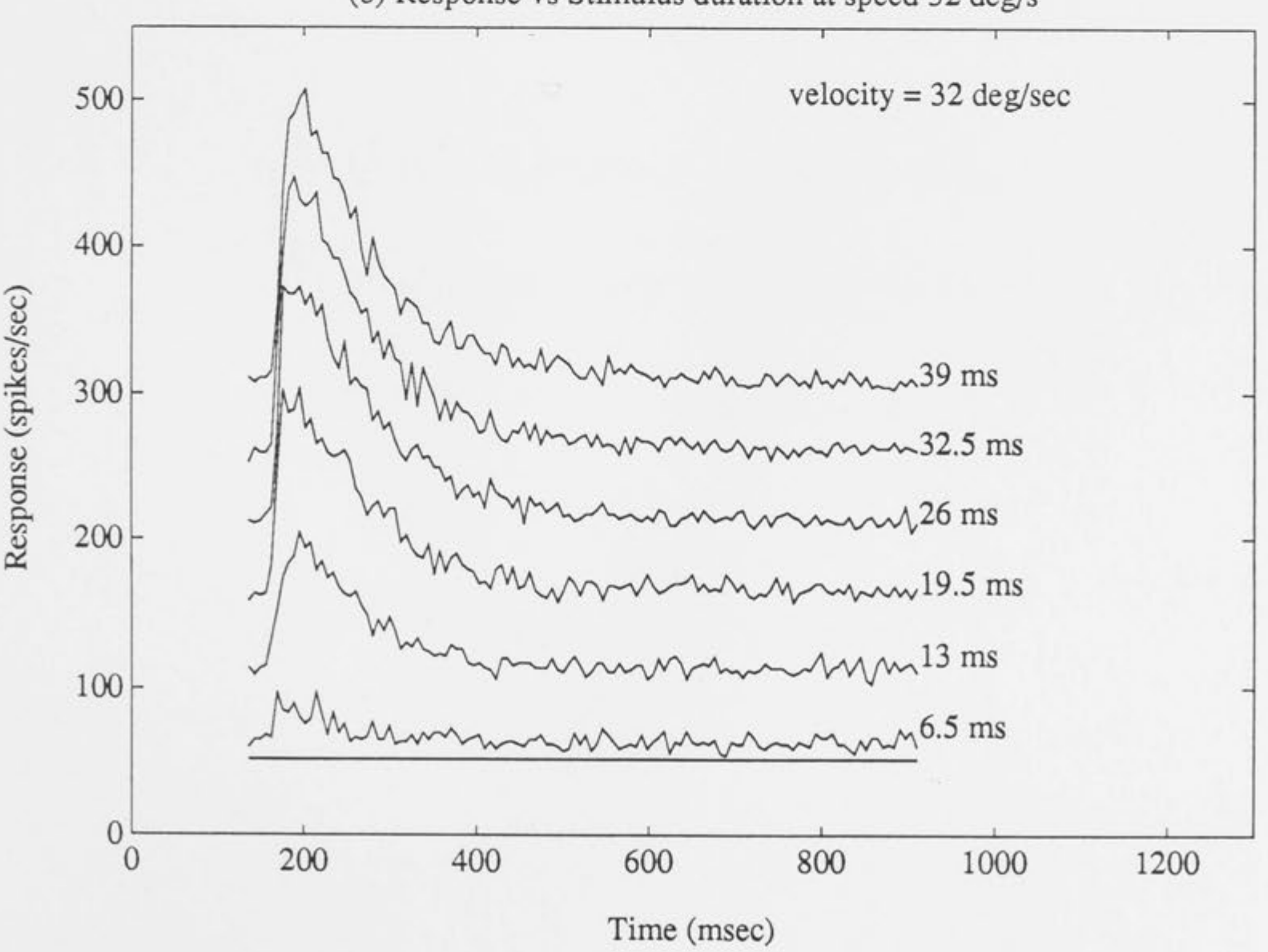
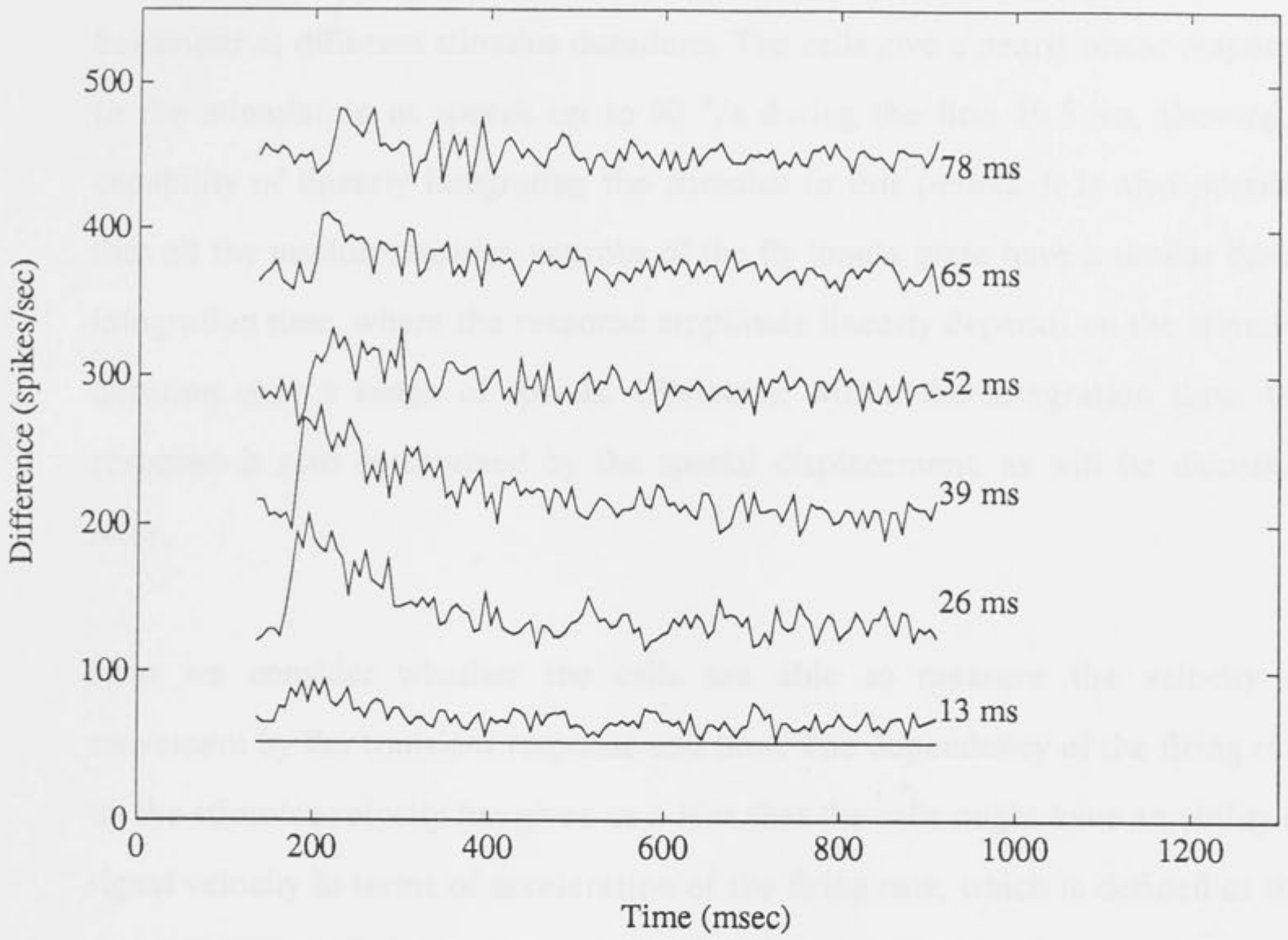
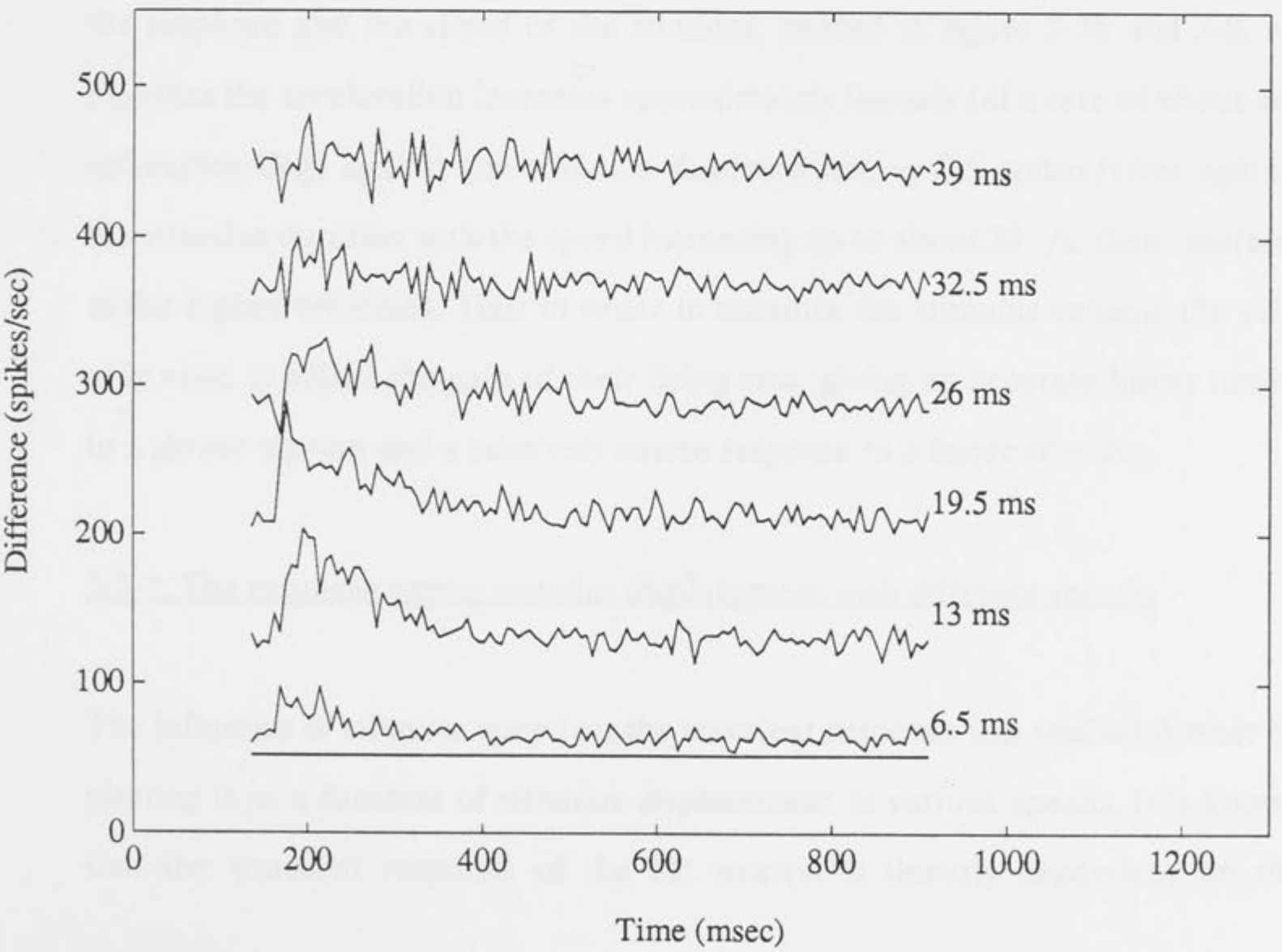


Figure 3-6. (c) and (d). The incremental response at each moment, measured by subtracting the response before this moment from the response at each moment of the stimulus, versus the stimulus time. This measurement shows the additional response of the neuron to the motion at a certain moment, which increased from the time 6.5 ms to the time 19.5 ms at speed 32 °/s or from 13 ms to 39 ms at speed 16 °/s, then decreased as the stimulus time increased. Actually, after a motion of 39 ms at speed 32 °/s the neuron gave no incremental response to the movement, which suggests that the neuron is interested only in a fresh movement.

(c) The incremental vs Stimulus time at speed 16 deg/s



(d) The incremental vs Stimulus time at speed 32 deg/s



An average integration time of 19 ms is obtained by analyzing the response behaviour at different stimulus durations. The cells give a nearly linear response to the stimulation at speeds up to 80 °/s during the first 19.5 ms, showing a capability of linearly integrating the stimulus in this period. It is also possible that all the motion sensitive neurons of the fly lobula plate have a similar linear integration time, where the response amplitude linearly depends on the stimulus duration over a range of speeds. Obviously, within the integration time, the response is also determined by the spatial displacement, as will be discussed later.

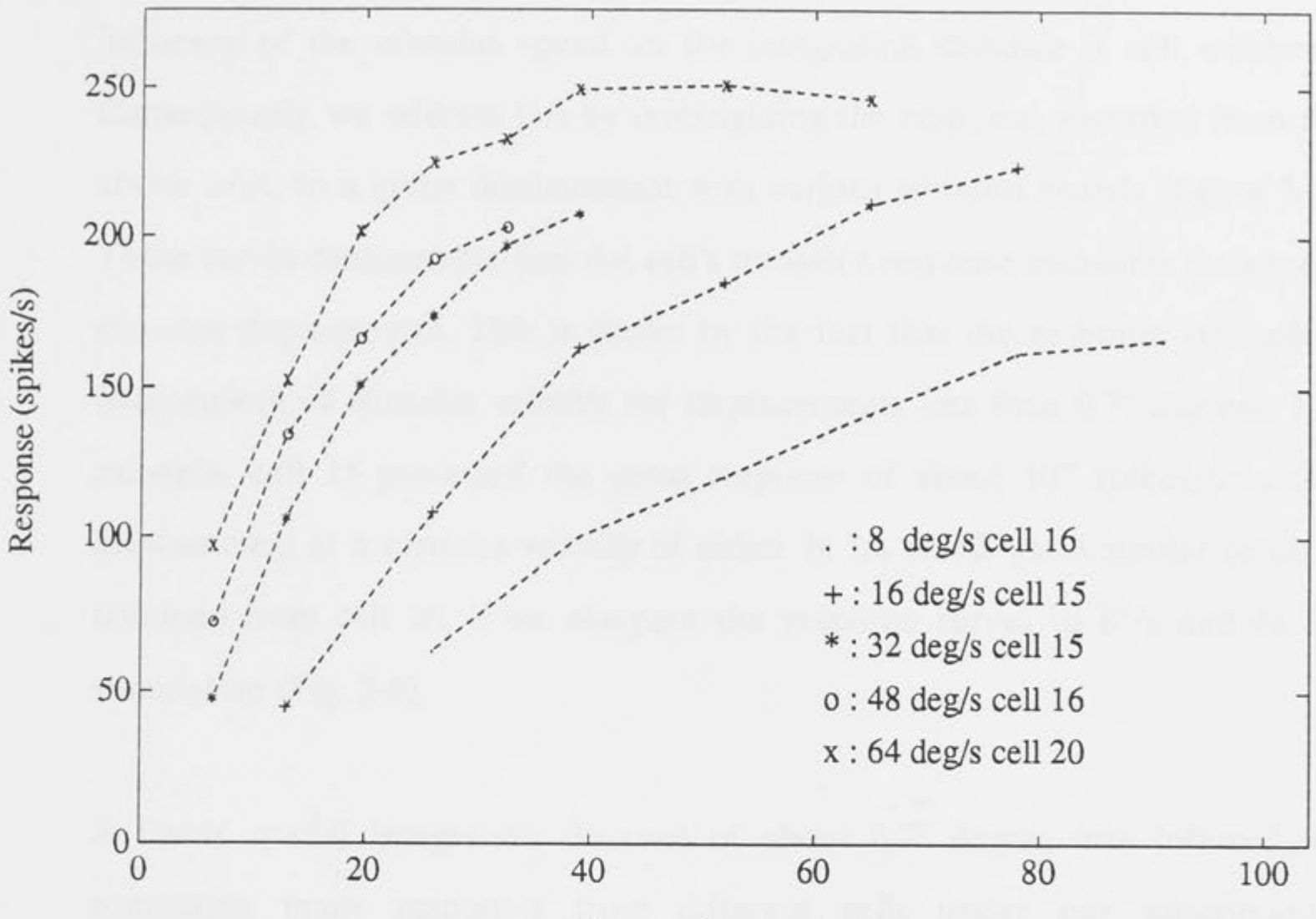
Next we consider whether the cells are able to measure the velocity of movement by the transient response and how. The dependency of the firing rate on the stimulus velocity has given us a hint that the cells might have an ability to signal velocity in terms of acceleration of the firing rate, which is defined as the rate of change of the response during the initial period. A faster motion will elicit a sharper slope. Looking at the relationship between the acceleration of the response and the speed of the stimulus, plotted in figure 3-7b and 3-8, we find that the acceleration increases approximately linearly (at a rate of about 180 spikes/sec/deg) against the stimulus displacement, or 7.5 spikes/s/ms against the stimulus duration with the speed increasing up to about 32 °/s, then saturates at the higher velocities. Thus in order to measure the stimulus velocity the cells only need to adjust the gain of their firing rate, giving an accurate linear tuning to a slower motion and a relatively coarse response to a faster stimulus.

3-3-7. The response versus stimulus displacement with different speeds.

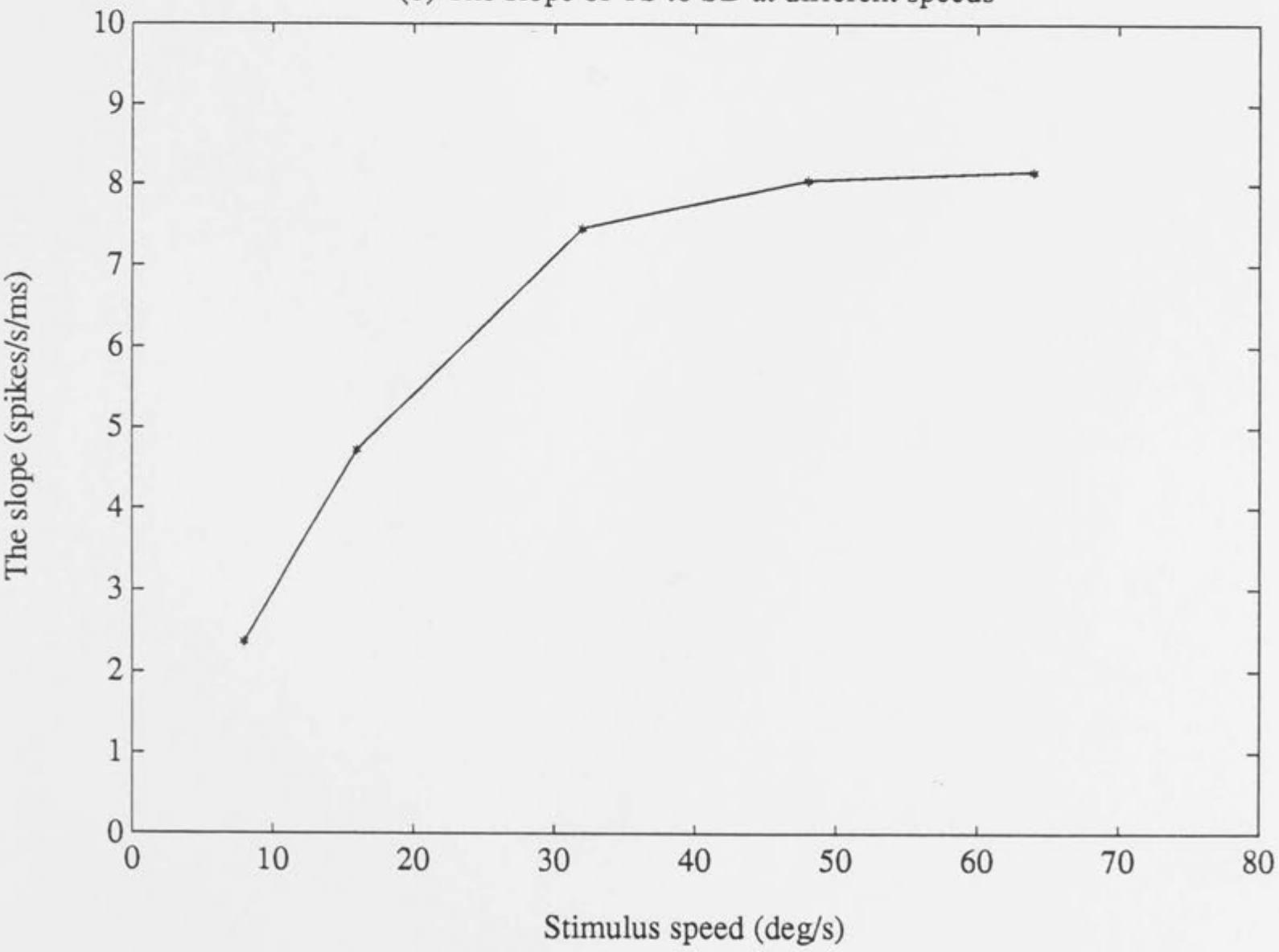
The influence of stimulus speed on the transient response was studied further by plotting it as a function of stimulus displacement at various speeds. It is known that the transient response of the H1 neuron is linearly dependent on the

Figure 3-7. (a). The influence of stimulus speed on the response is further studied by plotting the transient response (TR) versus the stimulus duration at different speeds in V2 neurons. The stimulus is a sine wave grating of spatial frequency 0.15 cyc/deg and contrast 0.3 moving at various speeds as shown. As the duration increased, all responses increased nearly linearly, then saturated. The neurons also gave a bigger response and saturated at a higher level to a faster movement. The dependency is shown in (b). The slope of TS to SD is measured as a ratio of the response initial increment at a certain speed (as in Fig. 3-6, c, d) to the stimulus duration. As the speed increased the slope also increased monotonically from 8 °/s to about 50 °/s then saturated, which suggests that the neuron responds in a graded way to the onset of movement at different speeds.

(a) Transient response (TR) vs stimulus duration (SD)



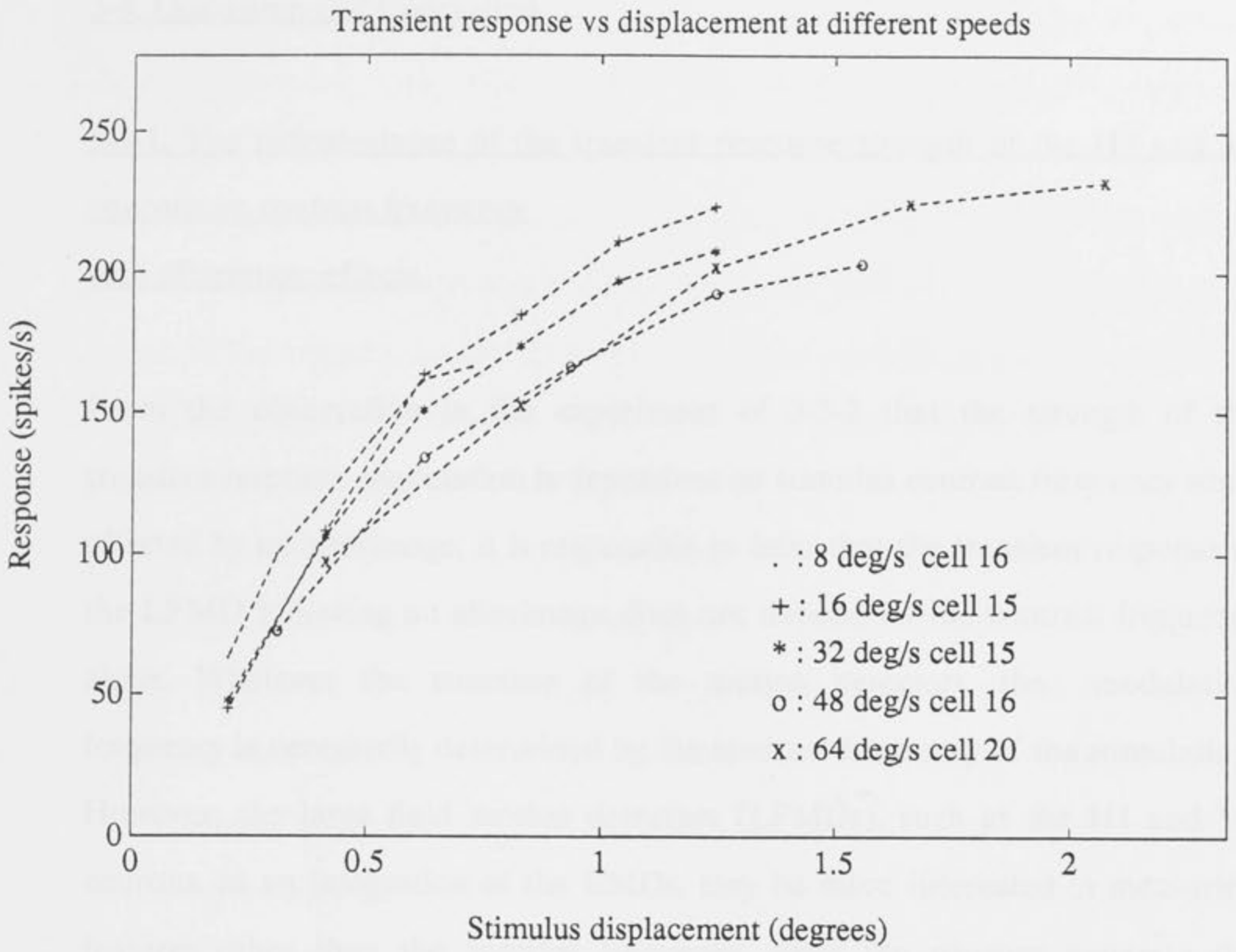
(b) The slope of TS to SD at different speeds



displacement within the spatial integration distance (Srinivasan 1983), but the influence of the stimulus speed on the integration distance is still unknown. Consequently, we address this by investigating the response, recorded from the above cells, to a given displacement with various stimulus speeds (figure 3-8). These curves demonstrate that the cell's transient response measures mainly the stimulus displacement. This is shown by the fact that the response strength is independent of stimulus velocity for displacements less than 0.7° degrees. For example, cell 15 produced the same response of about 107 spikes/s to 0.4° displacement at a stimulus velocity of either 16 °/s or 32 °/s. A similar result is obtained from cell 16, if we compare the response curves to 8°/s and 48 °/s stimulation (Fig. 3-8).

A linear spatial integration distance of about 0.7° degree was inferred, by comparing many responses from different cells under our experimental conditions. Within this distance all the transient responses have an initial slope of about 180 spikes/sec/deg irrespective of the stimulus speed and duration.

Figure 3-8. The transient response versus the displacement at different speeds. In figure 3-6, the response strength depends on the distance that the grating moved. This conclusion is now confirmed in further by plotting the transient response against the stimulus displacement. The transient response is a monotonic function of the stimulus displacement up to about 1 degree, irrespective of the stimulus speed and duration. We can define a linear spatial integration distance of 0.7°; over this distance the neuron always produces a response which is dependent linearly only on the stimulus displacement, irrespective of the speed and duration of movement. The responses saturated at a high level when the grating moved more than 2°, in strong contrast to a bar movement, in which the response dropped down for distances larger than 2° with the same motion conditions (see Fig. 4-10)


Transient response vs displacement at different speeds
Response (spikes/s)
Stimulus displacement (degrees)
0
50
100
150
200
250
0
0.5
1
1.5
2
. : 8 deg/s cell 16
+ : 16 deg/s cell 15
* : 32 deg/s cell 15
o : 48 deg/s cell 16
x : 64 deg/s cell 20

3-4. Discussion and Conclusion

3-4-1. The independence of the transient response strength of the H1 and V2 neurons on contrast frequency with afterimage effects.

From the observation in the experiment of 3-3-2 that the strength of the transient response modulation is dependent on stimulus contrast frequency when affected by an afterimage, it is reasonable to infer that the transient response of the LFMD following an afterimage does not depend on the contrast frequency alone. Whatever the structure of the motion detectors, the modulation frequency is necessarily determined by the contrast frequency of the stimulation. However, the large field motion detectors (LFMDs), such as the H1 and V2 neurons, as an integration of the EMDs, may be more interested in measuring features other than the contrast frequency, since the neurons generate the different strength of transient response to stimuli which are of the same contrast frequency but with different spatial frequency-velocity combinations. All results suggest that the basic task of the LFMDs is probably to count the number of passing edges for the preferred direction, which is in agreement with Horridge's suggestion (1990). First of all, the EMD's must give a great concern to the spatial structure of a moving object, producing a stronger response to a proper angular size of stimulus. That is why the response strength is not exactly determined by contrast frequency. The reason is simple, that the spatial structure characteristics are the most essential parameters which will decide the final behaviour of the animal, which must pay more attention to a small slowly closing object than to a big, fast moving, but far away background, even though both appear to have the same contrast frequency. In fact, in our experiment the neuron always gives a bigger response to a stimulus with a spatial frequency of 0.07 cyc/deg than to one of 0.28 cyc/deg. The speeds did not make a significant difference to the

response strength, since we found in other experiments that the neurons cannot discriminate movements of 80 °/s and 320 °/s just in terms of firing frequency.

This dependence on spatial structure may be due to the limitations of the motion detectors imposed by the structure of the compound eyes. The spatial wavelength of the stimulus is close to twice the interommatidial angle, approximately 0.28 cycles/degree. If there are lateral effects, such as lateral inhibition of any kind, with the spacing of the interommatidial axes, then spatial frequency can have an influence independent of contrast frequency. The higher the spatial frequency, the stronger the lateral inhibition that might be elicited, so that the cells must chose a proper size object as the target of interest, which may work in a similar mechanism as found in fly lamina cells in which the strength of the flanking inhibitory regions of the receptive fields of fly lamina cells decreases as the mean luminance is lowered (Pinter, Osorio & Srinivasan 1990). Finally, temporal integration may be also involved in forming the dependence upon spatial structure during the motion detection. Since, within the integration time, the response strength of the LFMDs depends on the displacement distance, they produce a bigger response when more stimuli are passing across the receptive field. This is just another indication that the response strength of the LFMDs is dependent on the number of passing edges.

3-4-2. A possible feed back loop during motion detection.

In the experiment of 3-3-3, the afterimage effects are strongly dependent on the prior-motion of the stimulus. In other words, the response is affected by the response history. It has been observed that the response strengths decrease and the time constants become shorter or the temporal bandwidth becomes wider, with increase of the prior-motion speed.

This result, of course, has several possible explanations; but the most likely one is that there is a feed-back loop in the fly's motion detection system. The afterimage effects are probably introduced at the level of the EMDs and are further influenced by a feed back loop before they are integrated in the large field motion detectors, H1 and V2. The signals or the responses to a prior-motion are fed back to adjust the cells present response, which leads to a decrease of the response gain and increase of the temporal bandwidth, as is typical of a feed back loop.

After long period of adapting to prior-motion, all low-pass temporal filters, presumably at the input level of the EMDs, are at least partly saturated, so that the firing modulation caused mainly by the low-pass filter becomes weak. Theoretically, the low-pass filter can oscillate the firing frequency of the EMDs in the transient response, but as described by Egelhaaf's model (1989) it can neither change the bandwidth of the response nor shift the response phase. However, We do see such changes in the experiments, therefore the afterimage effect is most likely not a feature of the EMDs with a low-pass filter alone. This conclusion is also supported by the fact that the decay constant of the afterimage depends on the speed of prior-motion, which obviously cannot be explained by use of a low-pass filter whose time constant is invariable. However, a feed back loop can provide a sufficient explanation because it can indeed change the time constant of a system.

Of course, in functional terms, the afterimage effects can be considered as a kind of low pass temporal filter but with a variable time constant, which will reduce the temporal resolution of the motion detectors when the environment is relatively stationary. This influence is eliminated in a moving environment; in the other words the temporal resolution will be improved by abolishing the afterimage effects when the animal is moving. So, with an afterimage the

response amplitude of the EMDs may be determined just by the difference between the present stimulus contrast frequency and the previous adapting contrast frequency some time ago. Undoubtedly this is a very important aspect of motion detection, because this kind of comparison or differential has the properties of a short term movement memory. Thus the motion detector might also be able to measure velocity and the change in velocity for a constant spatial frequency.

3-4-3. The influence of afterimage on directional selectivity of the LFMDs.

An interesting feature has been found in the experiment of 3-3-4, i.e, without the afterimage effects the response strength decreases as the stimulus phase drift is near to half a wave length for each (6.5 ms) frame, ie. directionality is retained. In contrast, with the afterimage effects the response does not decrease in the same way, ie. the directional-sensitivity of the neurons is reduced by the afterimage. So if the neuron, affected by afterimages, was still directionally sensitive, its response should be reduced and the modulation should be weaker to a faster moving pattern because that would appear to move in the opposite direction. But in fact the strength of modulation remained similar for all testing speeds, so obviously the directional-sensitivity of the cell has been lost when it is affected by an afterimage. Of course, this loss is only temporary because the afterimage lasts only for about 10 seconds (Maddess 1986). During this period the cells mainly measure the illuminance contrast between present and previous stimuli. The afterimage appears to occur before, and to inhibit, the detection of directional motion.

In fact, in the same experiment, another phenomenon relative to lateral interaction has been observed. The negative phase in the response already appeared when the stimulus speed was over 160 deg/s, which was close to about

one sixth of the wave length in each frame time, or jump of about 1.1° degree in each 6.5 ms (see Fig. 3-5). The appearance of negative phase in the response to a fast stimulus must reflect some unknown characteristics of the LFMDs in assembling the EMD's responses. It obviously needs explanation, of which one candidate is lateral inhibition. Supposing there is a lateral inhibition between individual EMDs, so that an obvious lateral inhibition can be generated only when lateral interaction from the preceding units is over a threshold during the integration time. The activity of the next EMDs will now be inhibited, causing a negative phase. This mechanism would depend on the distance moved during the integration time at the moment of the speed change. The faster the motion, the stronger the inhibition, so the deeper the negative phase. A 1.1° degree of minimum effective range also supports this assumption, since it is approximately equal to the radius of an individual EMD's receptive field which also indicates that the lateral inhibition comes from the neighbouring units.

CHAPTER FOUR

SPATIAL PROPERTIES OF THE LFMDS

THE RESPONSES OF H1 AND V2 TO A SINGLE MOVING BAR

Abstract

In this chapter, the spatial characteristics and measurement of the H1 and V2 have been investigated by brief jumps of a black bar with or without prior-motion. These two neurons treated as outputs of a motion detection system consisting of many distributed EMDs in parallel. In the experiments, a receptive field about 1.2° wide at half response height is observed from the plots of transient response strength against jump angle for both H1 and V2 (see 3-3-7), confirming again that both kinds of cells assemble signals from similar EMDs. When stimulated with prior-motion the cells exhibit sigmoidal-shaped transient response curves, in sharp contrast to the bell-shaped response curves produced by the stimulus without prior-motion. Those phenomena raise the possibility that the motion detection system may use two kinds of mechanisms to transform motion signals. One kind is a high-pass channel with a bell-shaped response curve, mainly interested in velocity changes, the other is a low-pass channel with sigmoidal-shaped response curve, which is active in continued movements and may serve fine velocity tuning. By considering a possible existence of short-term memory and lateral interaction and a feed back loop in flies visual system, it is now proposed that the right kinds of motion channels are most likely selected by switch cells according to the previous motions of objects. From the result that the ratio of the response contrast to the stimulus velocity contrast remained constant, irrespective of the changes in velocity, it is postulated that the LFMDs

abstract velocity contrast in responses to movements. Finally, it is found that the temporal discrimination of the cells is improved in responses to jumps with prior-motion since the response latencies are shortened by an average 6 to 10 ms.

4-1. Introduction.

4-1-1. The review of previous results.

As described in chapter 3, the responses to gratings reveal much about afterimages. Afterimages affect only the transient part of the wide-field motion detectors, when temporal resolution and directional selectivity are reduced.

In addition, some temporal and spatial properties of the directional motion-detection cells are investigated, especially the relationship of their responses to the stimulus velocity, duration and the displacement distance. The data described above (see 3-3-7) suggests that the linear integration distance of the cells is about 0.7°, and an average integration time is about 19 ms.

It has been shown that the motion detectors have similar temporal and spatial parameters in the responses to horizontal and vertical motion, and at low frequency they respond to every edge that passes their receptive fields, as proposed by Horridge (1990). It is already clear from the large fields of motion detectors and their high sensitivity to small movement that both horizontal and vertical neurons integrate the inputs from a large number of elementary motion detectors (EMDs). A postulated feed back loop would help to explain why temporal resolution and the range of temporal frequency-response of the neurons are increased in response to a stimulus with prior-motion, which might result in increasing the range of velocity which the cells can encode.

4-1-2. Adaptation of the response.

As shown by others (Maddess 1986), adaptation to the step stimulus enables the H1 neuron to respond better to a faster rate of stepping, and the response adapts more rapidly with faster repetition of the steps. Similarly, at greater stimulus velocities the response falls more steeply from the initial peak to a steady state. In fact, the faster or more frequently that the stimulus moves the faster the neuron adapts to it and therefore is better placed to respond rapidly when the stimulus is repeated. The decay constant of the adaptation ranges from 10 to 300 ms, depending on the velocity of the stimulus prior to a step, with velocities in the range 100 deg/s to 0.4 deg/s. The time constant of adaptation is determined locally in the visual field. A separation of the adapting stimulus and test stimulus by only 3.6 deg was sufficient to be out of range (Maddess & Laughlin, 1985). On the other hand, the increase in adaptation rate clearly is propagated rapidly but locally in front of an advancing stimulus, or these effects would not occur.

The Dutch work (de Ruyter van, Steveninck et al., 1986) was done after that of Maddess & Laughlin with slightly different results, I have also repeated this work on the fly Lucilia in Canberra with the following results. Moving stimuli increase the rate of adaptation more effectively than pure flicker. The responses are insensitive to spatial phase composition. The effect saturates with contrasts of 0.33. The adaptation rate is not determined by the spike rate of the H1 neuron itself, but by its inputs. The general conclusion is that the H1 neuron adapts to motion in much the same way that photoreceptors adapt to intensity, by saturation and increase of their dynamic range. The H1 neuron responds more strongly to an increment of velocity about the adapted value than it would in the unadapted state. In our experiments, similar results were found in V2 neurons.

4-1-3. Outline of the problem.

In nature, the fly must be interested in individual objects. Probably, the major function of its motion detection system is tuned to respond to movement of individual targets, such as tracking a prey or escaping from an antagonist. The parallel arrangement of numerous EMDs may be best suited to this kind of mission.

So now it is necessary to turn our attention to the responses to movements of a single target, and look again at the contribution of single motion detectors as they feed into the network structure of the large field motion detection system. The questions now concern the size of the EMDs receptive field, the linear response-displacement distance as well as the response integration time, and the possibility of lateral interactions between neighbouring EMD's and different kinds of signal channels. Once again the stimulus history turns out to be important.

The experiments in this section were designed to reveal the spatial properties of motion detectors, independent of the temporal domain. In fact many experiments already have been done on transient characteristics of motion detection, of which the majority focused on the temporal, rather than the spatial properties. We cannot ignore the possibility that previous results were affected by influences from the temporal domain, such as adaptation or saturation, so the question arises as to what the real spatial stucture is, and how this can be inferred from the transient responses of the motion detectors.

4-1-4. A single moving bar - a proper stimulus.

Although many results have been obtained already by using an extended grating in previous experiments, it is possible that extended stimuli are inadequate for characterising the responses of individual EMDs to isolated targets and for revealing the local interactions between the EMDs. The investigations with gratings seem to be related only to the properties of the motion detectors in response to movement of the background, and also the concurrent activity or silence of neighbours may influence the response of an individual EMD.

A single narrow bar apparently is a suitable stimulus here, and has the big advantage that it can simulate natural target movements whilst avoiding influences such as the afterimages. If the jump of the bar is restricted to be within the domains of the linear spatial and temporal integration of the cell, the responses of the cell can be regarded as impulse responses which are a useful guide to the transient properties of the individual EMDs.

Furthermore, recordings of responses to a jumped stimulus have provided a practical way to do just what we want in this section. The stimulus was a single black bar of width approximately equal to that of the receptive field of a single EMD. The bar was moved from one position to another on the screen between frames in just 6.5 ms, which is presumably faster than the temporal resolution of the EMD. The optimum step distance was the interommatidial angle, which was 1.2 degrees. This simple stimulus differs from other stimuli so far used, in enabling us to investigate the real distribution of the receptive field of the motion sensitive neurons, and interactions from the adjacent units, without considering any influence from the temporal domain. Furthermore, it describes the temporal properties of the EMD's in the transient state without adaptation or possible afterimage effects.

4-2. Methods.

4-2-1. Animal and preparation.

All experiments were performed on wild-type female sheep blowfies, Lucilia cuprina, obtained from the CSIRO, Division of Entomology, Blowfly Genetics Group, Black Mountain, Canberra ACT.

At about 2-9 days post-emergent the animal was chilled for about 90 seconds to improve handling, and then immobilized with wax to an stand with its head bent forward about 60 degrees. After that, a small cuticular flap in the diameter about of 1 mm was gently removed with a very fine knife from the back of the left side head over the lobula complex. Then the exposed optic lobes were immediately flooded with an insect Ringer's solution. The connective tissue sheath over the lobula complex was torn, and removed with a fine metal hook so that an electrode could penetrate the surface without breaking or dimpling the lobula plate. In order to stimulate only monocular parts of the eye and point the right eye towards the CRT centre, the animal was rotated around its axis by 30 degrees. The animal sat 10 cm from the CRT, and the display area of the screen was in 10 cm by 10 cm. All flies were adapted to the CRT for about 10 minutes before recording. The recording room was kept dark and the temperature controlled to about 23° C.

4-2-2. Stimulus and recording.

The stimulus pattern used in this chapter was a single dark bar over a white background, either in the vertical or in the horizontal orientation, desplayed on a CRT unit (having a P31 phosphor) under control of an on-line computer (PDP-11-03) by assembly and DAOS programming languages. Spectral properties of

the display tube were given in Dvorak et al. (1975). By feeding appropriate commands to the computer, the position of the bar could be shifted along either the horizontal or the vertical direction either (a) instantaneously to cause a jump, or (b) by small steps at regular intervals to approximate continuous motion at different velocities. The width of the bar in most cases was fixed at 3.3° visual angle, which just covers the receptive field of a single EMD. The position of the bar was kept at the centre of the screen so that in each trial the stimulation is approximately to the same EMDs. The screen refresh time was 6.5 ms, which is short enough to keep the stimulus period in the integration time, and a frame contained 1024 lines. The equipment was virtually the same as that of my previous experiments in chapter 3.

Extracellular recordings from the large-field directionally-selective motion-detecting neurons (H1 and V2) in the lobula plate were made using tungsten-in-glass electrodes. The spikes from the neurons were amplified by 10 times with a pre-amplifier P-16, collected by the computer via a Schmitt-trigger interface, then averaged histograms were generated and stored in the computer. More recently, the data were transferred to an Apollo-10000 work station for further analysis.

4-3. Experimental results.

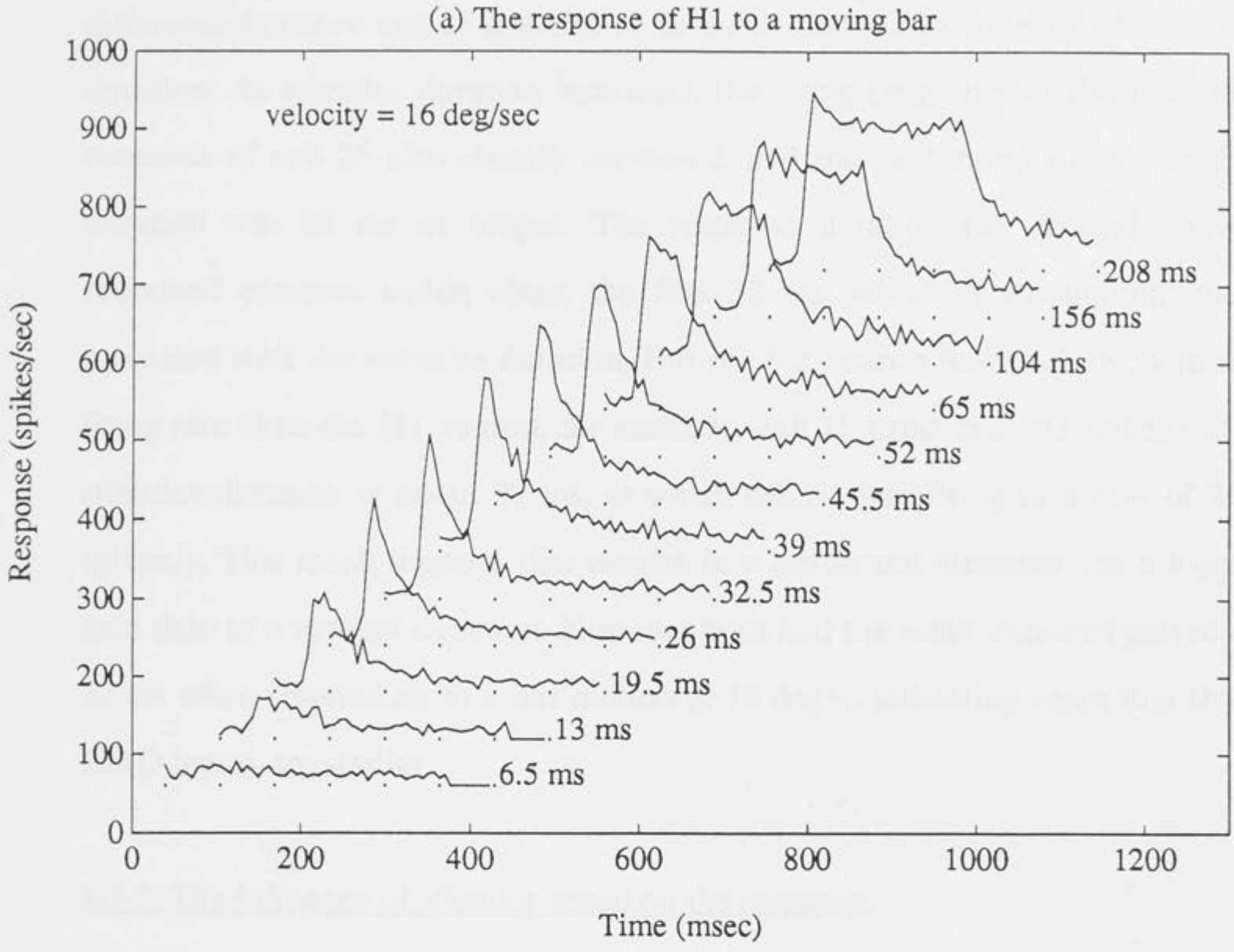
The responses of about 80 H1 and V2 neurons from the lobula plate of the fly to motions of a single dark bar are described in this chapter, including the responses to a single jump or to a continued motion, with or without prior-motion. All are presented as Post-Stimulus-Time-Histograms averaged about 100 times.

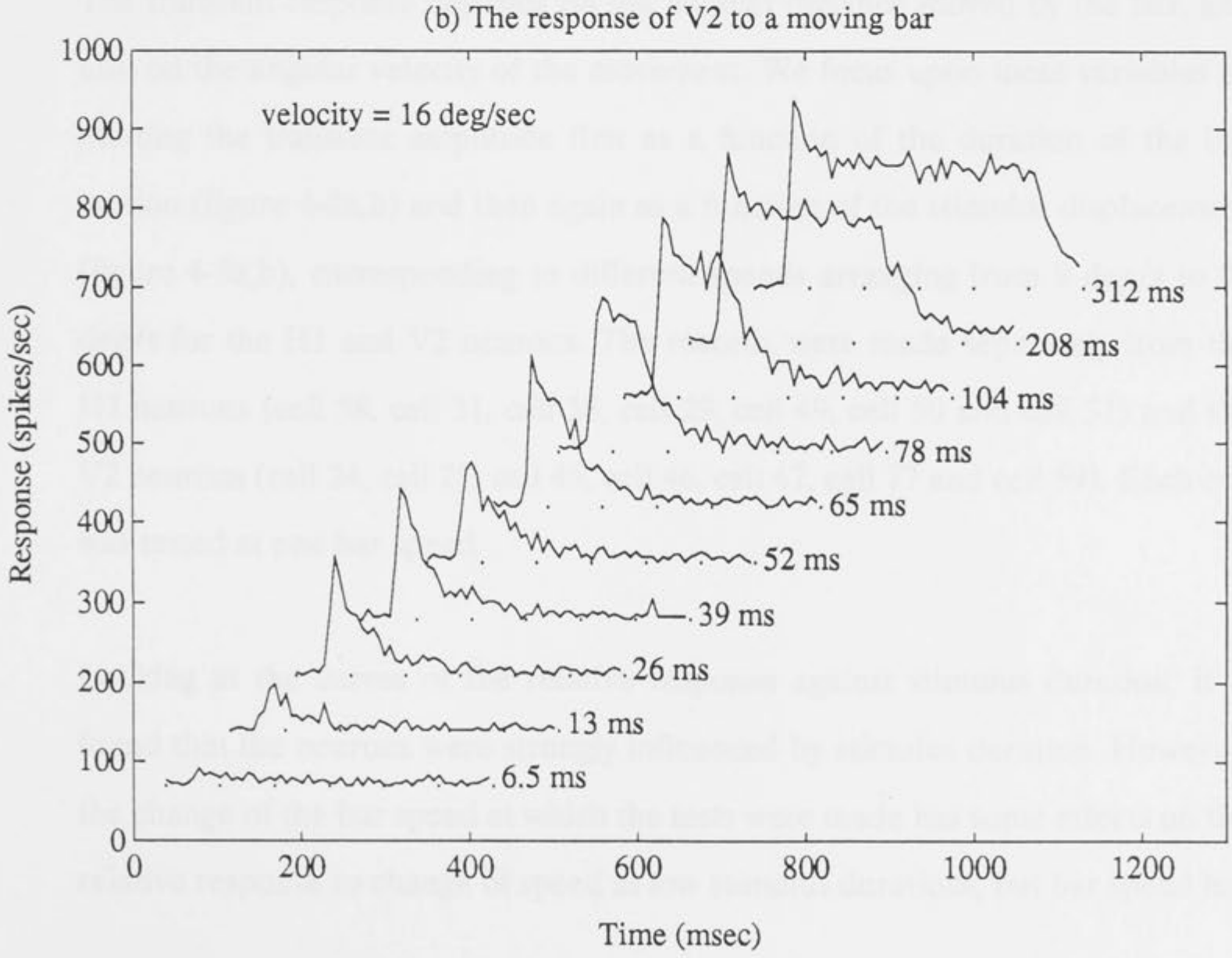
4-3-1. The time course of responses to bar movements at one speed.

We first look at an example of the time course of the response of the H1 neuron to bar movement at one speed but of varied duration. The stimulus was arranged so that a single dark bar 3.32° degrees across was moved at 16 deg/s for various durations from 6.5 ms to 208 ms. The response (cell 31) was averaged over 100 repeats of the stimulus to give post-stimulus histograms (Psth), as shown in figure 4-1a. The response consisted of an initial transient peak with approximately exponential fall to a steady maintained level. The duration of the transient period was defined arbitrarily as that part of the response which increased only in amplitude without change in the response width. It was found that, as the stimulus duration increased from 6.5 to 208 ms, the response amplitude within the first 32.5 ms of the stimulation first increased nearly linearly from about 24 spikes/s to 207 spikes/s, while the duration of the transient response remained remarkably constant at about 32 ms. After this 32 ms period the transient response became saturated and a constant sustained response of 163 spikes/s was obtained for all stimulus durations. Finally the response duration widened to be almost equal to that of the stimulus.

As a comparison, the response of the V2 neuron (cell 25) was recorded under the same stimulus conditions as cell 31 (figure 4-1b). There is no significant

Figure 4-1. Responses of the H1 and V2 neurons to a moving bar at speed 16 °/s. A black bar of width 3.32° remained at the centre of the screen for 2 seconds, then moved at a constant speed 16 °/s for various times, as shown. The response was averaged 100 times for each trail. There is little difference in the time course between the H1 and V2 responses; both cells gave a significant response to the motion of 13 ms, over three times higher than the background firing, indicating that the H1 and V2 neurons detect this stimulus (with 100 summations). The transient responses of both cells increased in height to a saturation level, but with an almost constant response duration as the stimulus duration increased to about 40 ms. Then, for stimuli longer than 70 ms, a steady state response appeared with the same width as the stimulus duration. The steady state response is lower than the transient response, indicating that H1 and V2 are high-pass neurons which detect changes in stimulus. In sharp contrast to the response to a moving grating, no oscillation in the response amplitude is observed, indicating that the response to a moving bar is nearer to the properties of the EMDs.


(a) The response of H1 to a moving bar
velocity = 16 deg/sec
208 ms
156 ms
104 ms
65 ms
52 ms
45.5 ms
39 ms
32.5 ms
26 ms
19.5 ms
13 ms
6.5 ms
Response (spikes/sec)
Time (msec)
0
100
200
300
400
500
600
700
800
900
1000
0
200
400
600
800
1000
1200


(b) The response of V2 to a moving bar
velocity = 16 deg/sec
312 ms
208 ms
104 ms
78 ms
65 ms
52 ms
39 ms
26 ms
13 ms
6.5 ms
Response (spikes/sec)
Time (msec)
0
100
200
300
400
500
600
700
800
900
1000
0
200
400
600
800
1000
1200

difference between cell 25 and cell 31 in the response as a function of stimulus duration. As stimulus duration increased, the firing frequency of the transient response of cell 25 also steadily increased, and then saturated when stimulus duration was 65 ms or longer. The response duration (as defined above) remained constant within about the first 32 ms period of stimulation, then increased with the stimulus duration. But the V2 neuron has a relatively lower firing rate than the H1 neuron, for example, cell 25 produced 163 spike/s at a stimulus duration of about 39 ms, at which cell 31 was firing at a rate of 220 spikes/s. This result suggests that motion in a horizontal direction has a bigger gain than in a vertical direction. However both had the same transient period of 32 ms when responding to a bar motion at 16 deg/s, indicating again that their EMD inputs are similar.

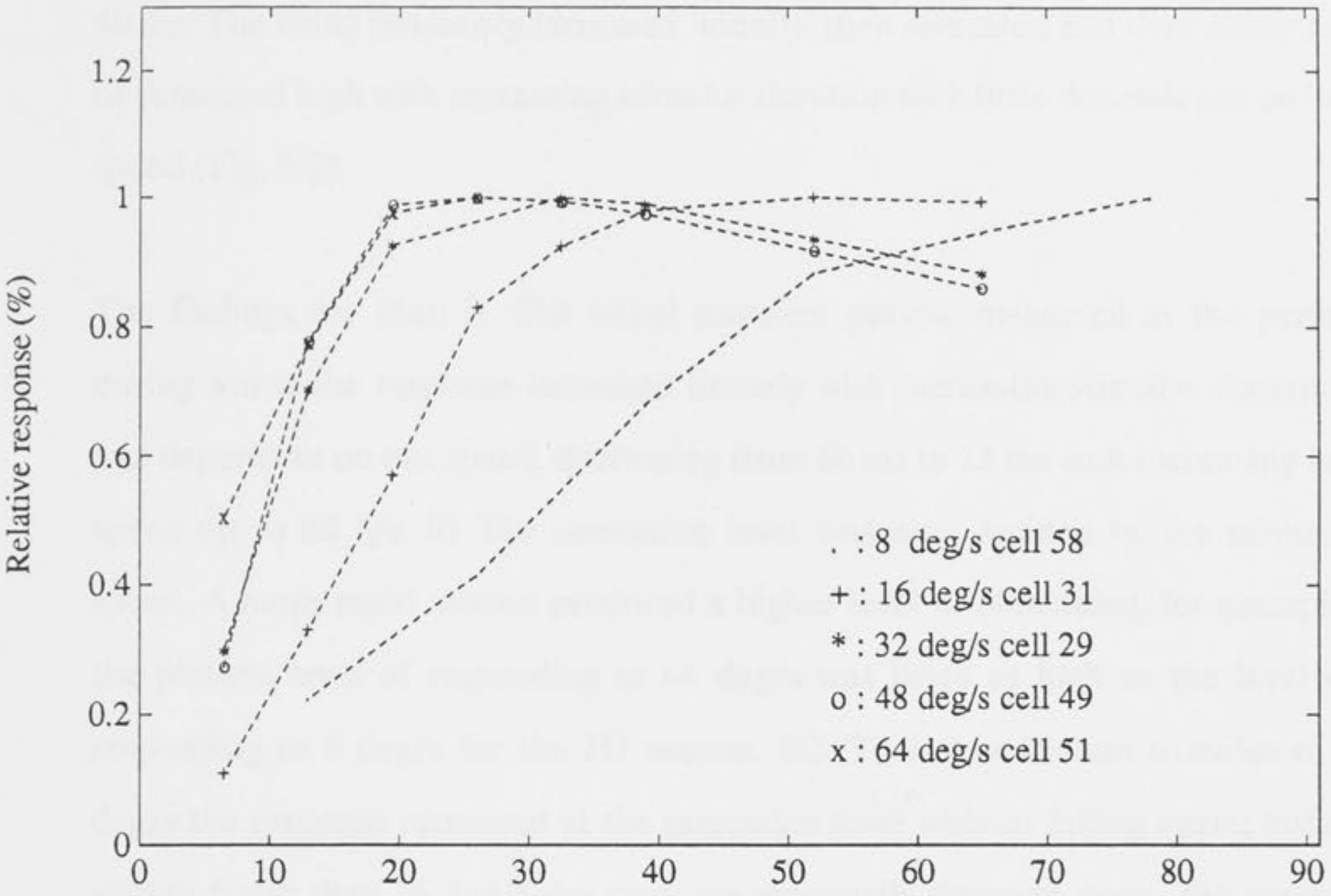
4-3-2. The influence of stimulus speed on the response.

The transient response depends on the angular distance moved by the bar, and also on the angular velocity of the movement. We focus upon these variables by plotting the transient amplitude first as a function of the duration of the bar motion (figure 4-2a,b) and then again as a function of the stimulus displacement (figure 4-3a,b), corresponding to different speeds arranging from 8 deg/s to 80 deg/s for the H1 and V2 neurons. The records were made separately from the H1 neurons (cell 58, cell 31, cell 38, cell 29, cell 49, cell 50 and cell 51) and the V2 neurons (cell 24, cell 25, cell 45, cell 46, cell 47, cell 77 and cell 59). Each cell was tested at one bar speed.

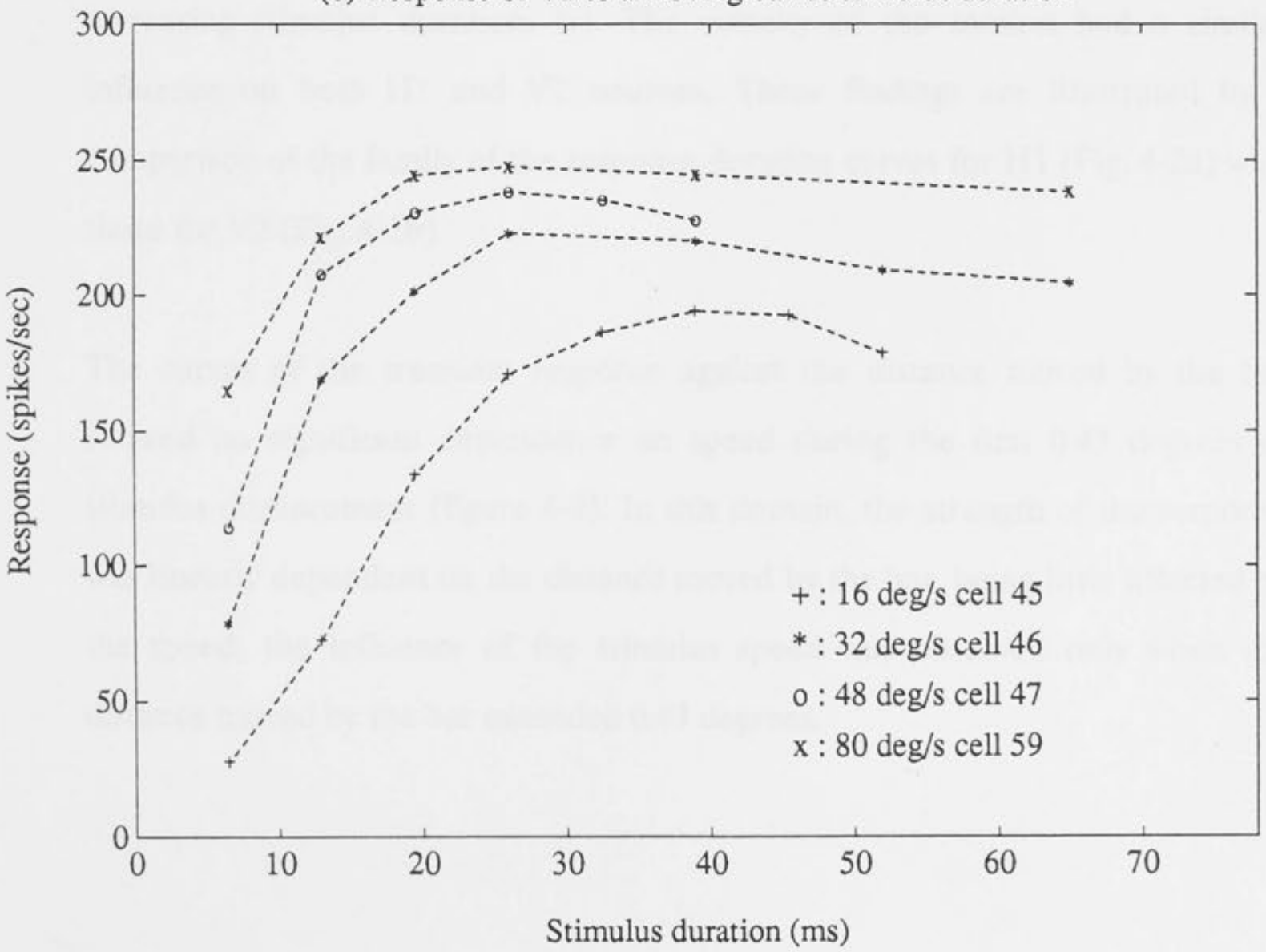
Looking at the curves of the relative response against stimulus duration, it is found that the neurons were strongly influenced by stimulus duration. However, the change of the bar speed at which the tests were made has some effects on the relative response to change of speed at low stimulus durations, but bar speed has

Figure 4-2. Transient responses of H1 and V2 neurons to a black moving bar versus the stimulus duration for different speeds, as indicated in the insets. As the stimulus duration increased, the responses of both kinds of neurons firstly increased, then saturated, and finally either remained at a high level (the H1 neurons, see (a)) or fell (the V2 neurons, see (b)). Apparently, the responses are strongly dependent on the velocity. The absolute strength of the responses to a fast motion is bigger than to a slow one (4-2b). The time to saturation is about 80 ms at the speed of 8 °/s, 40 ms at 16 °/s, and 30 ms at 32 °/s (4-2a & 4-2b). A critical speed of 48 °/s is found for both neurons, beyond which the neurons fired similarly in both response strength and the time to saturation.

(a) Response of H1 to a moving bar vs stimulus duration



(b) Response of V2 to a moving bar vs stimulus duration



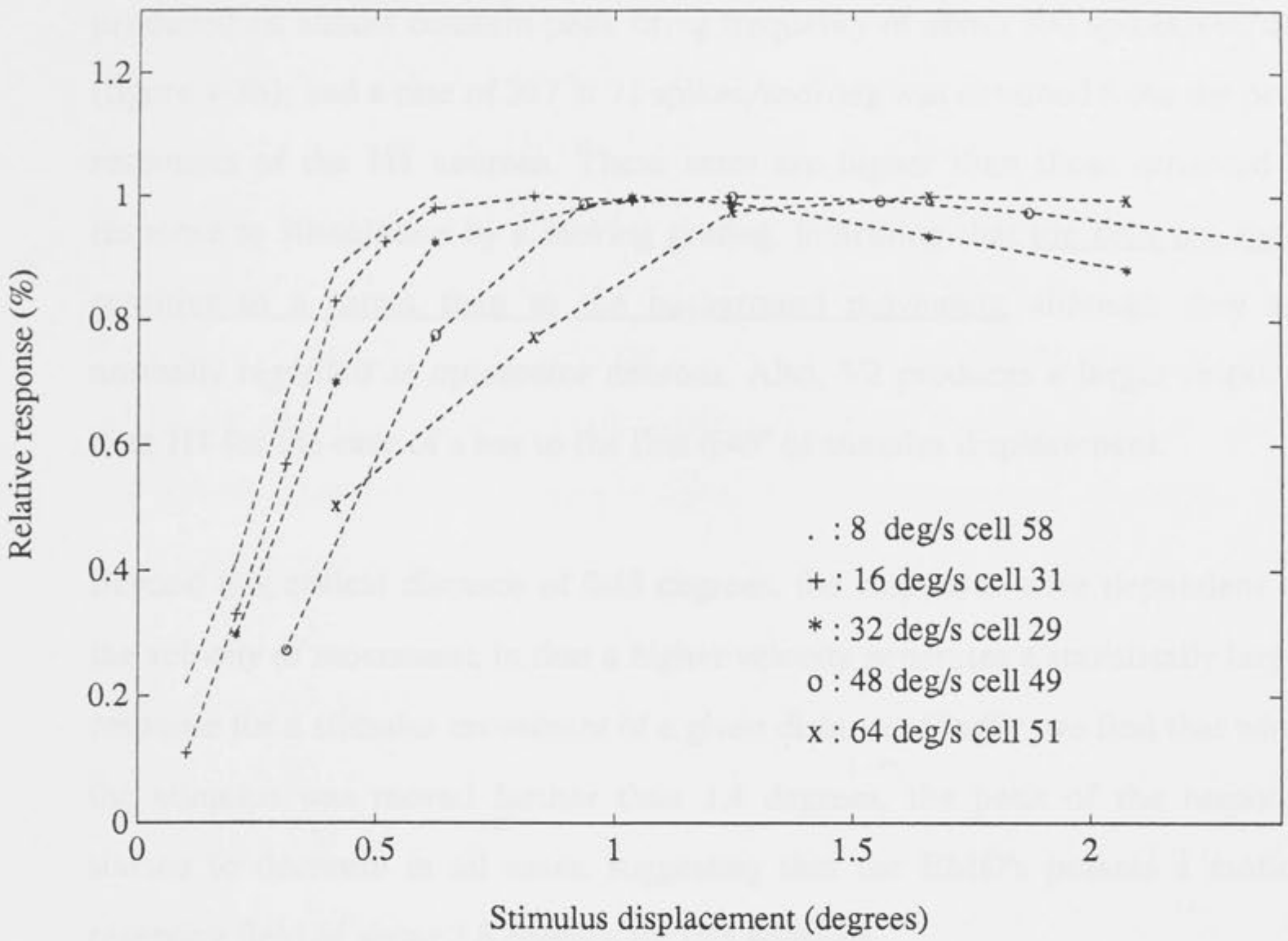
little effect on the response to change of speed for the stimulus durations above 40 ms. The firing frequency increased initially, then saturated and then either fell or remained high with increasing stimulus duration with little dependence on bar speed (Fig. 4-2).

The findings are that: i). The initial transient period, measured as the period during which the response increased linearly with increasing stimulus duration, was dependent on bar speed, decreasing from 60 ms to 13 ms with increasing bar speed up to 80 °/s. ii) The saturation level was also decided by the stimulus speed. A more rapid motion produced a higher level of plateauing, for example, the plateau level of responding to 64 deg/s was twice as high as the level of responding to 8 deg/s for the H1 neuron. iii). To a slow motion stimulus of 8 deg/s the response remained at the saturation level without falling again; but to stimuli faster than 16 deg/s the response eventually dropped down, the greater the speed, the faster it dropped down. This is in strong contrast to the findings with a grating stimulus (Fig. 3-7), where the responses never dropped with increasing stimulus duration. iv). The velocity of the motion had a similar influence on both H1 and V2 neurons. These findings are illustrated by a comparison of the family of the response-duration curves for H1 (Fig. 4-2a) with those for V2 (Fig. 4-2b).

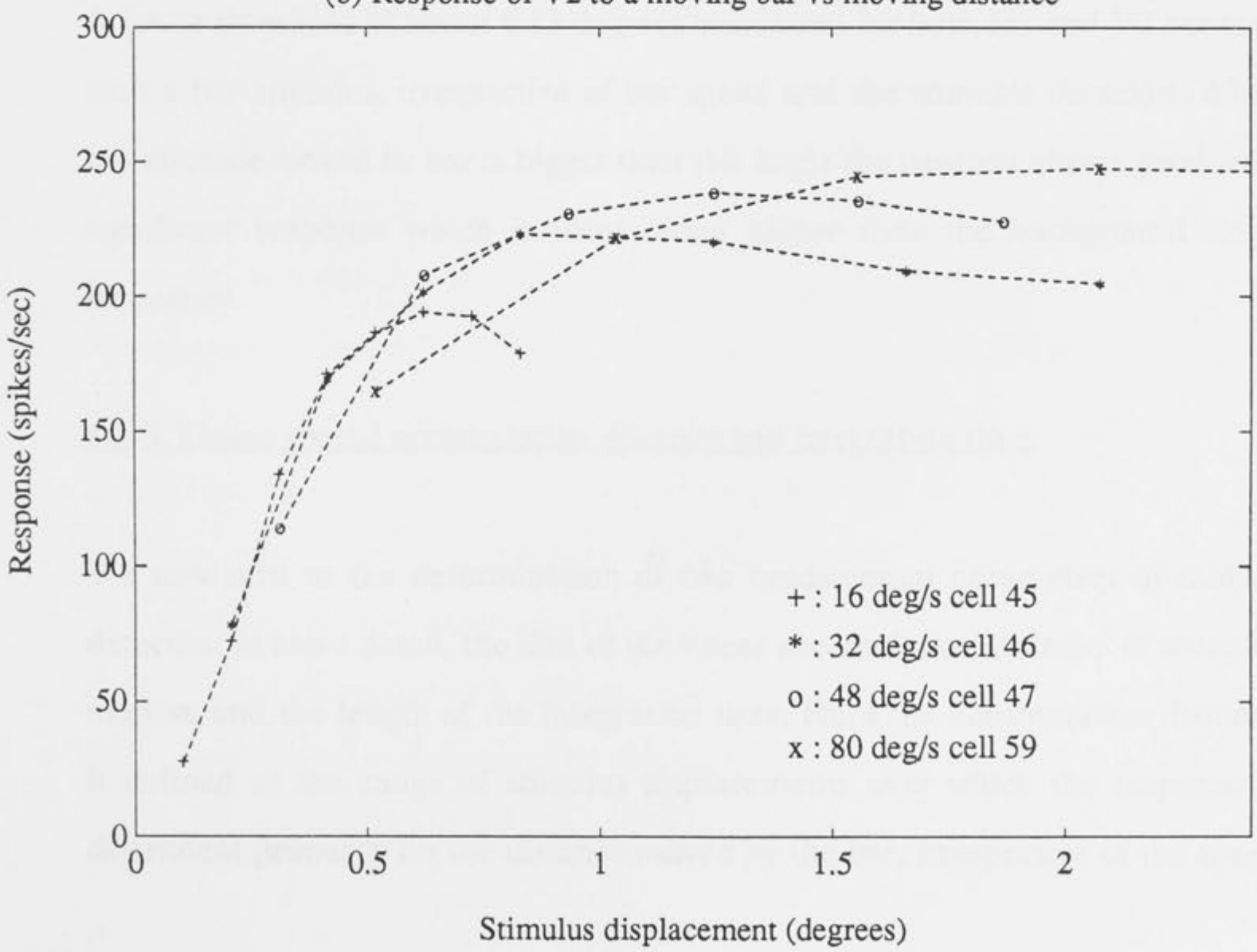
The curves of the transient response against the distance moved by the bar showed no significant dependence on speed during the first 0.43 degrees of stimulus displacement (figure 4-3). In this domain, the strength of the response was linearly dependent on the distance moved by the bar, being little affected by the speed; the influence of the stimulus speed was observed only when the distance moved by the bar exceeded 0.43 degrees.

Figure 4-3. The responses of (a) H1 and (b) V2 versus the bar displacement. The response data are the same as in Fig. 4-2, but now replotted against the angular distance of the bar movement. This figure demonstrates that the responses are linearly dependent on the stimulus displacement up to about 0.7°. The transient firing frequency depends on displacement, irrespective of the movement speed and duration. The responses were saturated after about 1.25°, which may reflect a spatial property of the EMD's.

(a) Response of H1 to a moving bar vs moving distance



(b) Response of V2 to a moving bar vs moving distance



While responding to the first 0.43 degrees of movement, the V2 neurons produced an almost constant peak firing frequency of about 390 spikes/sec/deg (figure 4-3b); and a rate of 307 ± 71 spikes/sec/deg was obtained from the peak responses of the H1 neurons. These rates are higher than those observed in response to stimulation by a moving grating, indicating that the cells are more sensitive to a target than to the background movement although they are normally regarded as optomotor neurons. Also, V2 produces a larger response than H1 for the case of a bar to the first 0.43° of stimulus displacement.

Beyond this critical distance of 0.43 degrees, the responses were dependent on the velocity of movement, in that a higher velocity generates a statistically larger response for a stimulus movement of a given distance. Finally, we find that when the stimulus was moved further than 1.4 degrees, the peak of the response started to decrease in all cases, suggesting that the EMD's possess a motion receptive field of about 2.8 degrees for this stimulus.

A lower threshold of about 0.13 degrees was found for both H1 and V2 neurons with a bar stimulus, irrespective of bar speed and the stimulus duration. When the distance moved by bar is bigger than this angle the neurons always produce a significant response which is three times higher than the background firing frequency.

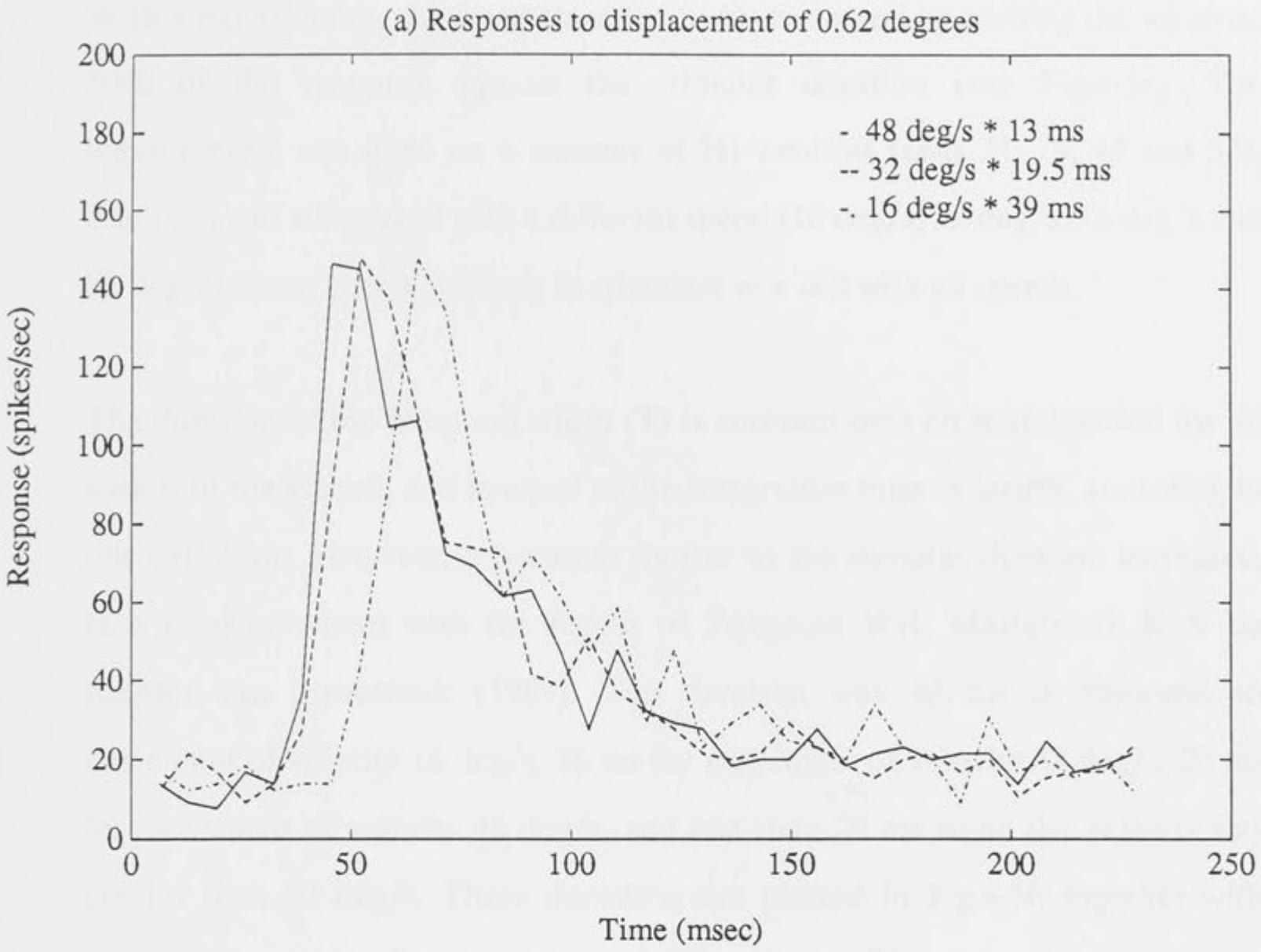
4-3-3. Linear spatial accumulation distance and integration time.

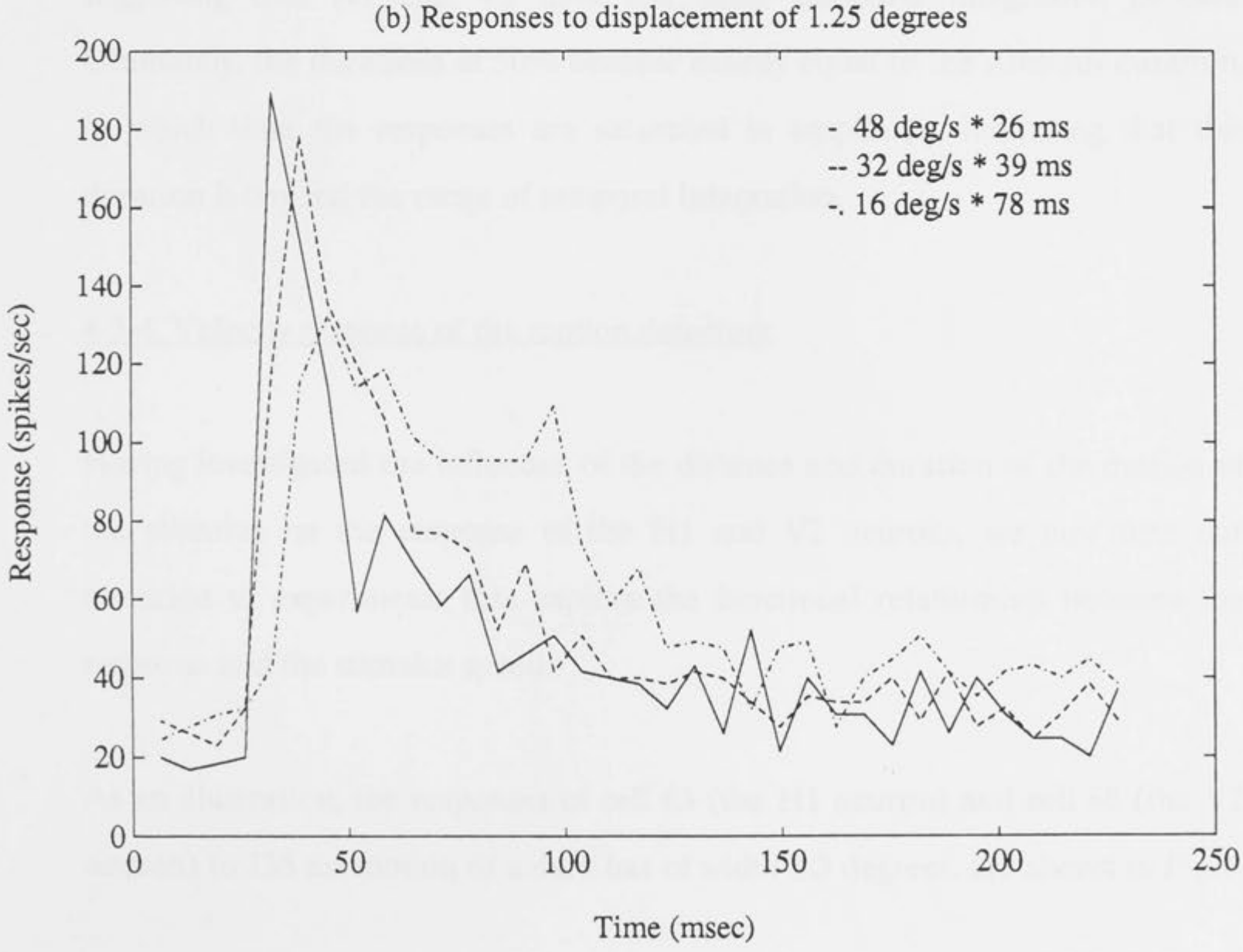
We now turn to the determination of two fundamental parameters of motion detection in more detail, the size of the linear accumulation distance of stimulus motion, and the length of the integration time. Here the accumulation distance is defined as the range of stimulus displacements over which the response is dependent primarily on the distance moved by the bar, irrespective of the speed

and duration of the movement. Thus, it is a direct measure of the range of the graded response to spatial displacements. The integration time is defined as (a) the period over which the response only increases in amplitude, without changing any of its temporal characteristics, as the stimulus duration increases. In fact, (b) the duration of the transient response at 50% amplitude, also called the integration time, which is also relevant in evaluating the temporal resolution. Constancy of response width, with the above stimulus conditions, is an indication that the mechanism is unable to discriminate different stimulus durations within this period. Thus integration time is a measure of the temporal resolution with respect to motion detection.

The measurement of the linear accumulation distance was performed in a V2 neuron (cell 37) by recording the response to fixed displacements with different combinations of the speed and stimulus duration. The displacement was first chosen to be 0.62 degrees, with the speeds set to 16 deg/s, 32 deg/s, and 48 deg/s, and the corresponding durations set to 39, 19.5, and 13 ms, respectively. The response was constant in amplitude for each of the three combinations of stimulation, differing only in the time to peak and the latency (figure 4-4a). A similar result was obtained from experiments with the H1 neuron. These experiments clearly demonstrate that the cells are able to accumulate response over a displacement up to 0.62 degrees in the spatial domain. Over this range of displacements, the cell responds by generating the same firing frequency in response to a given displacement, irrespective of the speed and the duration of the displacment. But, when a stimulus displacement of 1.25 degree was used, the different speeds of the bar produced big differences either in the amplitude or in the temporal parameters of the response (Fig.4-4b). Therefore the 1.25 degrees displacement obviously falls outside this range. In our most experiments the linear accumulation distance was around only 0.62 degree. This is small, and shows that the motion perception processes are local.

Figure 4-4. Demonstration of linear spatial integration distance. The responses were recorded from a V2 neuron to a black moving bar of width 3.3°. The pattern was moved in the preferred direction at various speeds as indicated in the insets to keep the distance moved at a constant of 0.62° (a); or 1.25° (b). When the neuron responded to a constant displacement of 0.62°, it always produced responses of similar strength, irrespective of the speed and duration (a). But when a 1.25° displacement was presented, the response strengths were significant by different (b). These facts indicate that over the first 0.62° of the stimulus the response strength indicates only the displacement. Therefore, the response strength can be considered as a linear integration over this angle. Obviously, the response to a distance of 1.25°, grater than this integration distance, is influenced by other factors, such as the speed. It is also apparent that the neuron produced a faster response to a more rapid motion.


(a) Responses to displacement of 0.62 degrees
- 48 deg/s * 13 ms
-- 32 deg/s * 19.5 ms
-. 16 deg/s * 39 ms
Response (spikes/sec)
Time (msec)
0
20
40
60
80
100
120
140
160
180
200
0
50
100
150
200
250


(b) Responses to displacement of 1.25 degrees
- 48 deg/s * 26 ms
-- 32 deg/s * 39 ms
-. 16 deg/s * 78 ms
Response (spikes/sec)
Time (msec)
0
20
40
60
80
100
120
140
160
180
200
0
50
100
150
200
250

With a bar stimulus, the integration time was measured by plotting the width at 50% of the response against the stimulus duration (see Fig.4-5a). The measurement was done on a number of H1 neurons (cells 31, 29, 48 and 51). Each cell was stimulated with a different speed (16 deg/s, 32 deg/s, 48 deg/s and 80 deg/s), since it took too long to stimulate one cell with all speeds.

The duration of the temporal width (T) is constant over an initial period for all speeds of the stimuli, and is equal to the integration time in length, according to one definition. However, it becomes shorter as the stimulus duration increased, in a good greement with the results of Zaagman WH, Mastebroeh K & de Ruytter van Steveninck (1983). The duration was 40 ms in response to movement of velocity 16 deg/s, 26 ms for movement of velocity 32 deg/s, 20 ms for movement of velocity 48 deg/s, and less than 20 ms when the velocity was greater than 80 deg/s. These durations are plotted in Fig.4-5b together with comparable results from a group of V2 neurons. The two curves coincide, suggesting that H1 and V2 have the same temporal integration process. Ultimately, the durations at 50% become exactly equal to the stimulus duration, by which time the responses are saturated in amplitude, indicating that this duration is beyond the range of temporal integration.

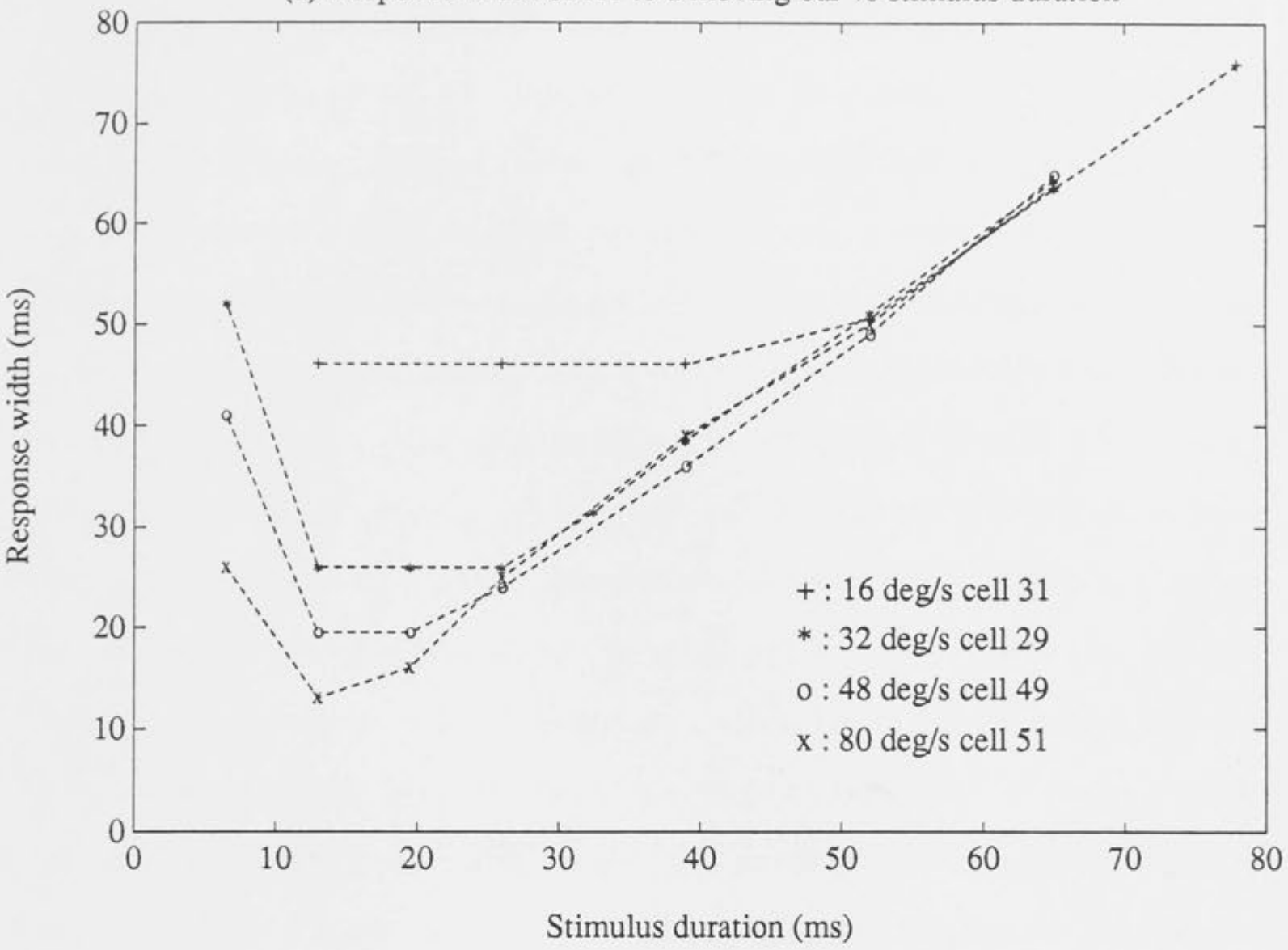
4-3-4. Velocity response of the motion detectors.

Having investigated the influence of the distance and duration of the motion of the stimulus on the response of the H1 and V2 neurons, we now turn our attention to experiments that explore the functional relationship between the response and the stimulus speed.

As an illustration, the responses of cell 63 (the H1 neuron) and cell 68 (the V2 neuron) to 135 ms motion of a dark bar of width 3.3 degrees, are shown in Fig.4-

Figure 4-5. (a) Response width, which is defined as a width at 50% of the response peak, versus stimulus duration. The measurements were done on a number H1 neurons which responded to a black bar of width 3.3° moving at the speeds ranging from 16 °/s to 80 °/s with a duration from 6.5 ms to 78 ms. As the stimulus duration increased, the response first remained a constant width for an initial period ($\underline{T}$) of the stimulus, then was the same duration as the stimulus. The time of $\underline{T}$ is dependent on the motion speed; for example, it is 20 ms when the stimulus is 48 °/s, and about 40 ms for a motion of 16 °/s. According to one definition of the integration time, during this period $\underline{T}$ the stimulus can be integrated by the neuron to give the response strength, but without changing the response temporal parameters, such as the width of the response and the time to peak. The relation between ($\underline{T}$) and the stimulus speed is plotted in (b), together with comparable results from V2 neurons. As the speed increased, the integration time of both neurons decreased exponentially from 65 ms at 8 °/s to about 20 ms at 80 °/s. The integration time is related to the temporal resolution, which is improved for faster motions.

(a) Response width of H1 to a moving bar vs stimulus duration



(b) Integration time of H1 and V2 vs stimulus speed

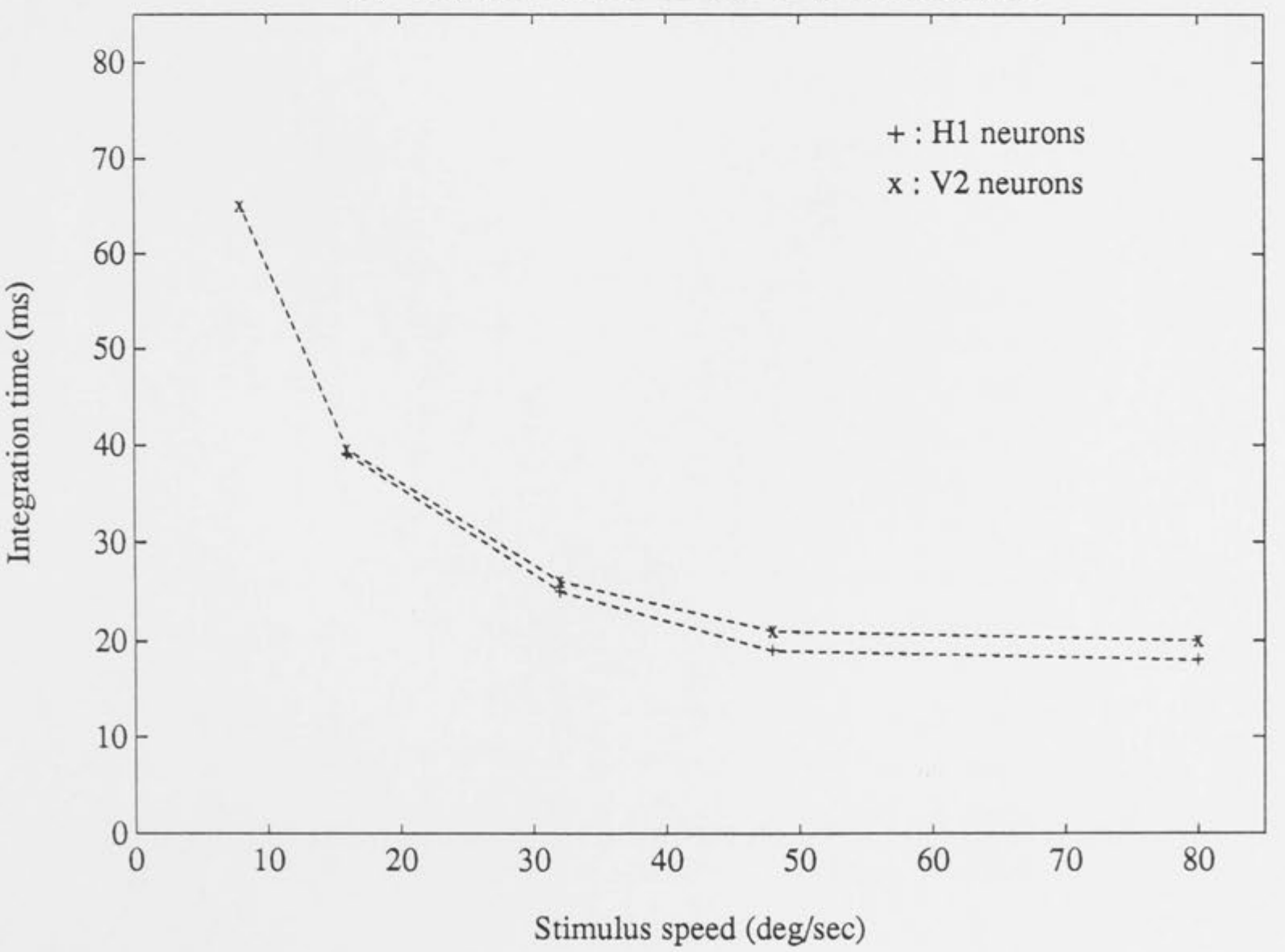
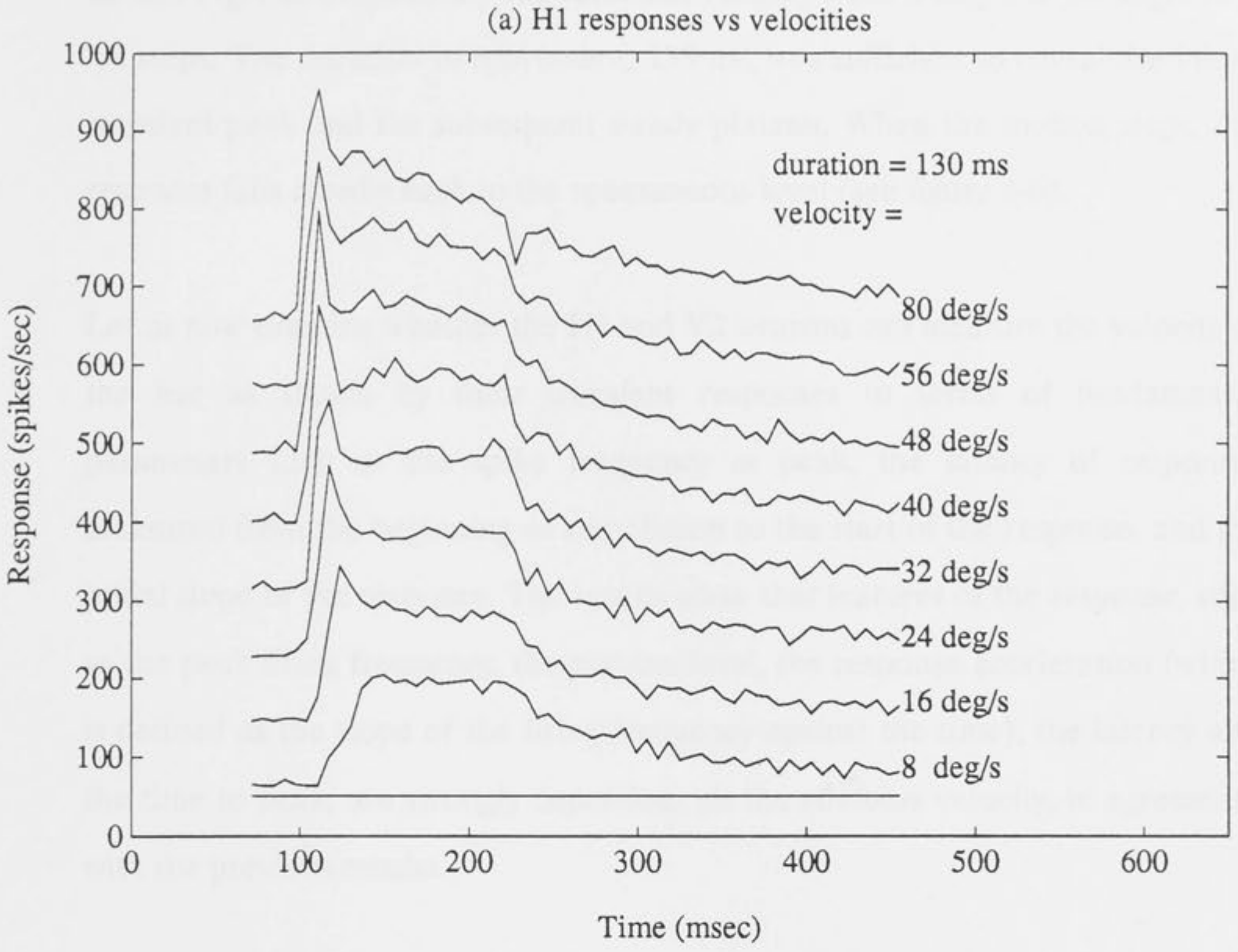
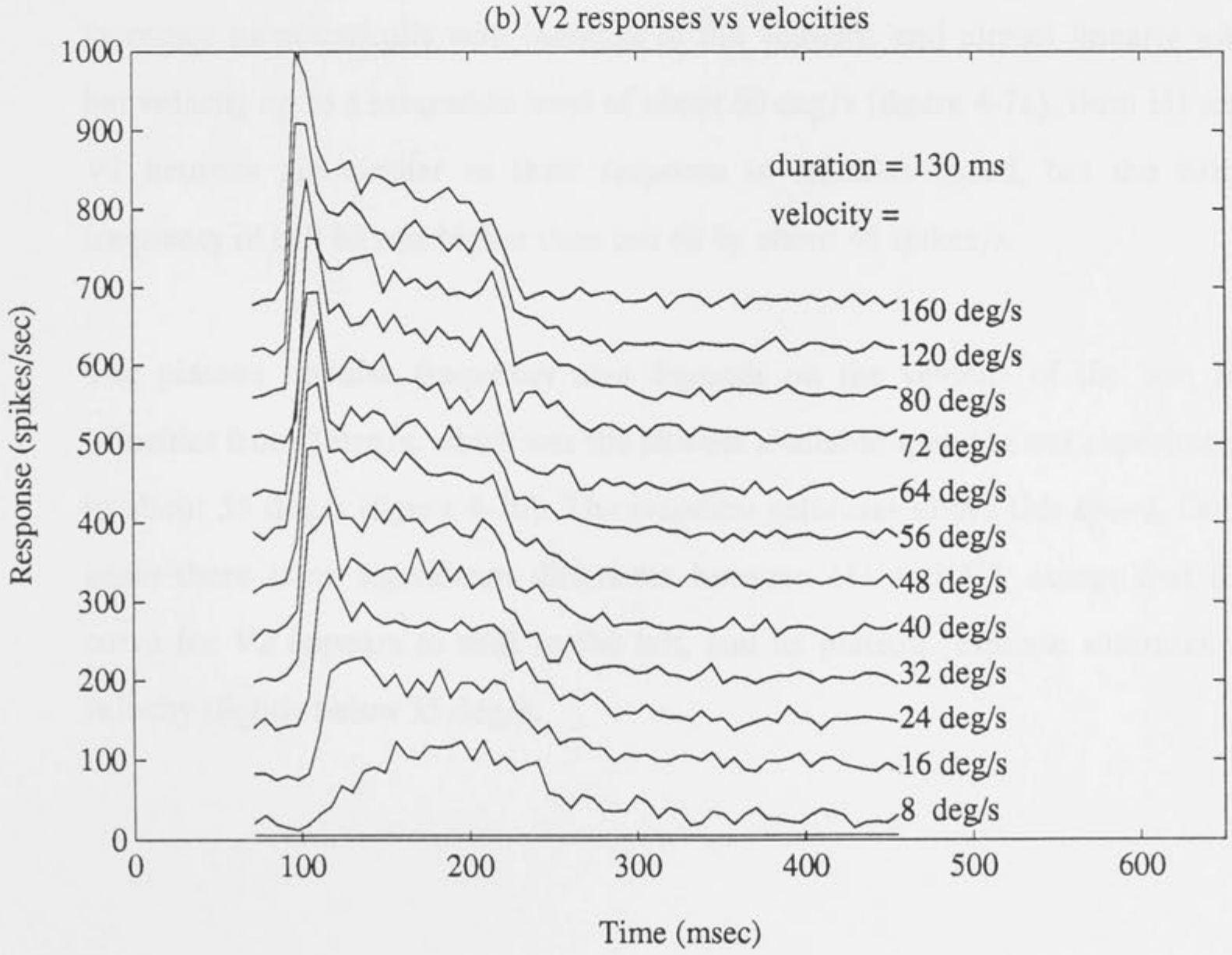


Figure 4-6. The responses of H1 and V2 versus stimulus velocities. The experiment was to test how one H1 and one V2 neuron responds to a black bar of width 3.3° at different speeds, as indicated, for 130 ms, which is long enough to reveal the properties of the neurons in both transient and steady states. As the speed of the bar movement increased, the responses changed their parameters, as the response strength increased and the time to peak as well as the latency shortened, particularly over a range from 8 °/s to 40 °/s. There is no significant difference between the H1 and V2 neurons. However, a slight, except at high speeds, especially over 80 °/s. The H1 neuron couldn't produce a response with separate transient and steady states as the V2 did, instead giving a negative phase at the moment the bar stopped. If the response indeed consists of two stages - the transient and steady states, it is probable that the record is a weighted summation of these two parts. When responding to a motion at low speed, for example at 8 °/s there is no transient peak in the response, suggesting a low-pass filter or channel. But above 16 °/s, there is a high transient peak in the response.


(a) H1 responses vs velocities
Response (spikes/sec)
1000
900
800
700
600
500
400
300
200
100
0
0
100
200
300
400
500
600
duration = 130 ms
velocity =
80 deg/s
56 deg/s
48 deg/s
40 deg/s
32 deg/s
24 deg/s
16 deg/s
8 deg/s
Time (msec)


(b) V2 responses vs velocities
Response (spikes/sec)
1000
900
800
700
600
500
400
300
200
100
0
0
100
200
300
400
500
600
duration = 130 ms
velocity =
160 deg/s
120 deg/s
80 deg/s
72 deg/s
64 deg/s
56 deg/s
48 deg/s
40 deg/s
32 deg/s
24 deg/s
16 deg/s
8 deg/s
Time (msec)

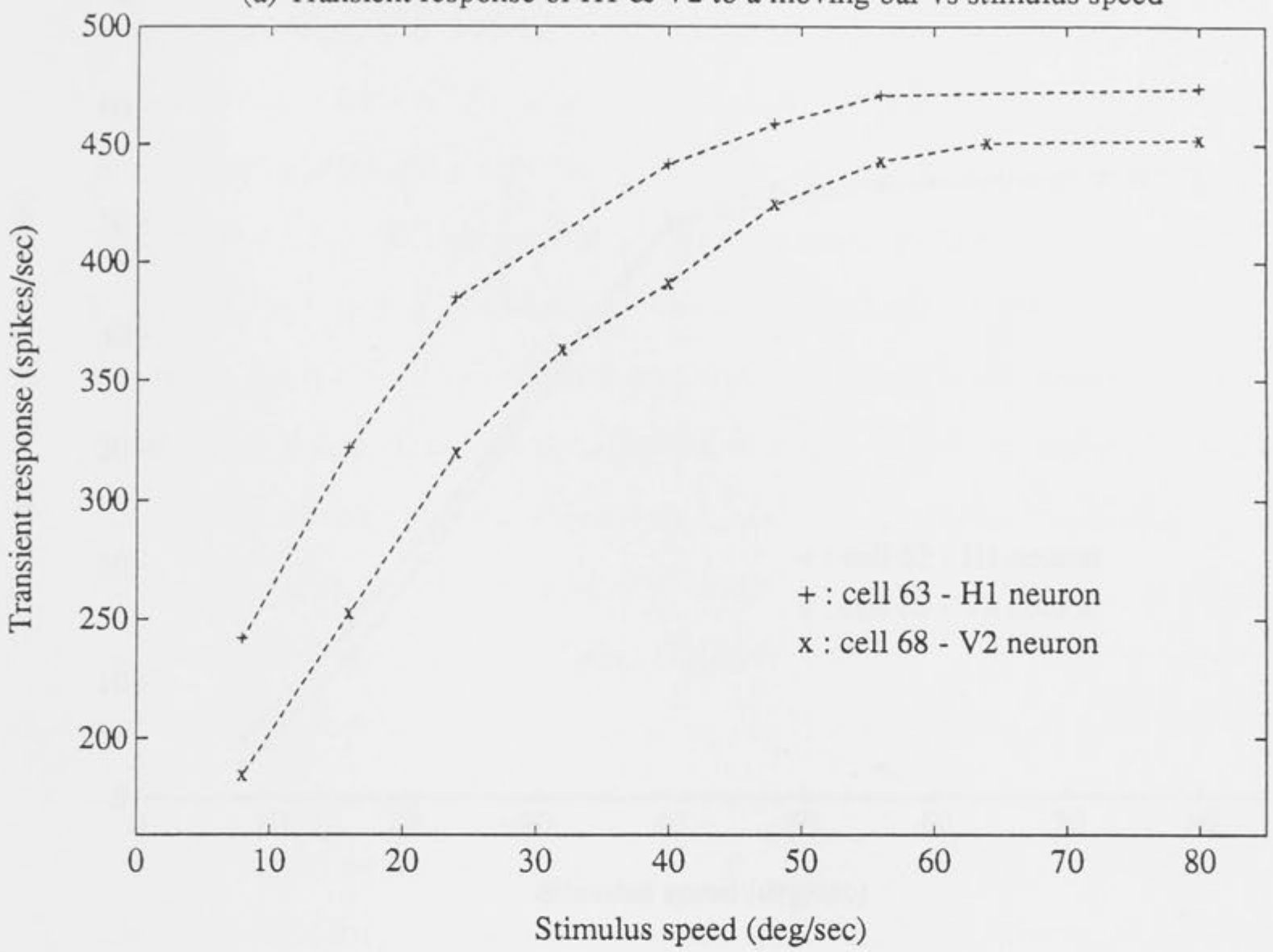
6a and Fig.4-6b respectively for velocities ranging from 8 deg/s to 80 deg/s in 8 °/s steps. The duration of movement, 135 ms, was sufficient to reveal the initial transient peak and the subsequent steady plateau. When the motion stops, the response falls rapidly back to the spontaneous level (see figure 4-6).

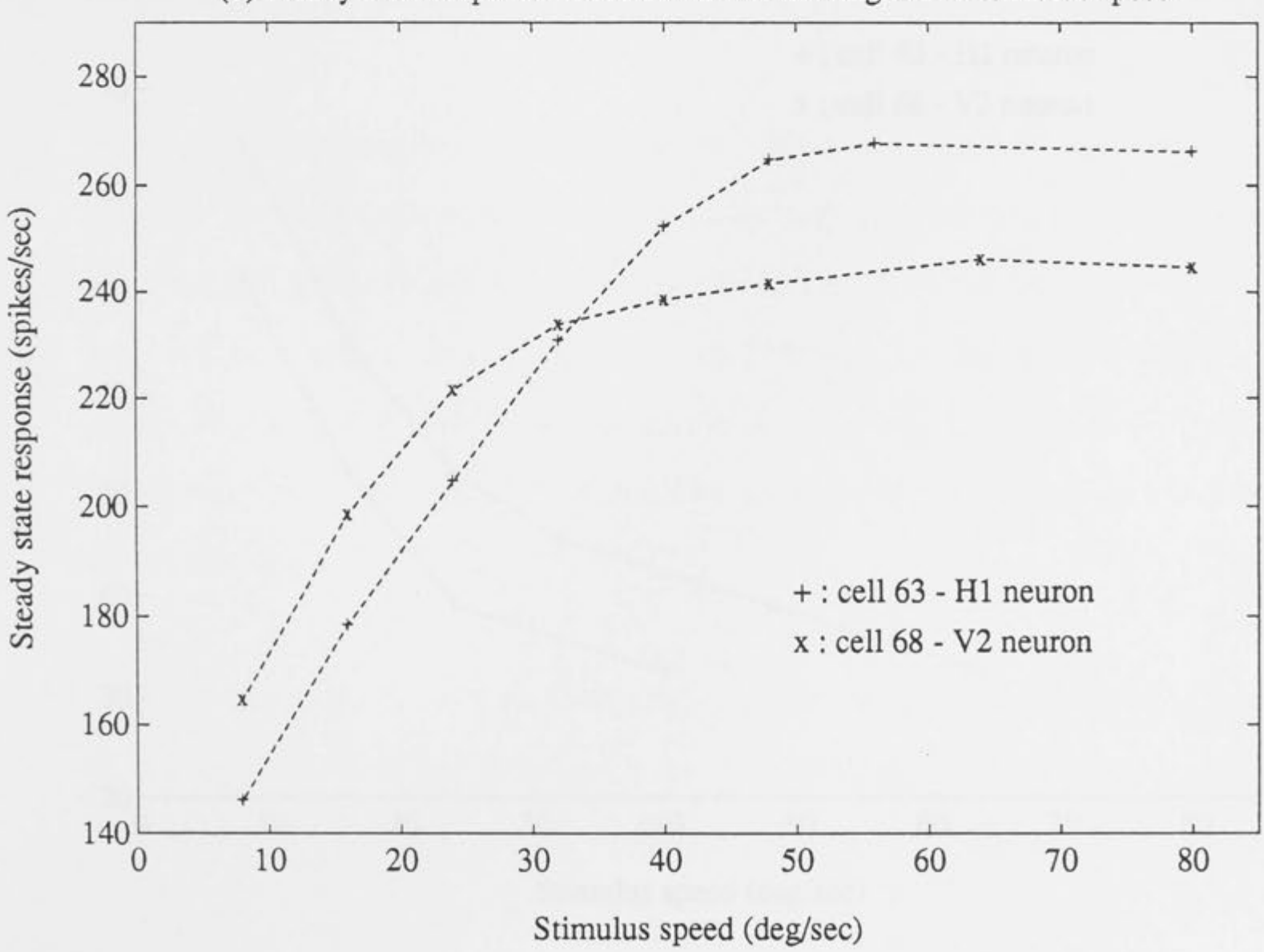
Let us now examine whether the H1 and V2 neurons can measure the velocity of the bar as shown by their transient responses in terms of fundamental parameters such as the spike frequency at peak, the latency of responses measured from the beginning of stimulation to the start of the response, and the initial slope of the response. The results show that features of the response, such as the peak firing frequency, the plateau level, the response acceleration (which is defined as the slope of the firing frequency against the time), the latency and the time to peak, are strongly dependent on the stimulus velocity, in agreement with the previous results.

For the bar stimulus the absolute firing frequency of the peak transient response increases monotonically with increase of the velocity, and almost linearly with bar velocity up to a saturation level of about 60 deg/s (figure 4-7a). Both H1 and V2 neurons are similar in their response to stimulus speed, but the firing frequency of cell 63 was higher than cell 68 by about 46 spikes/s.

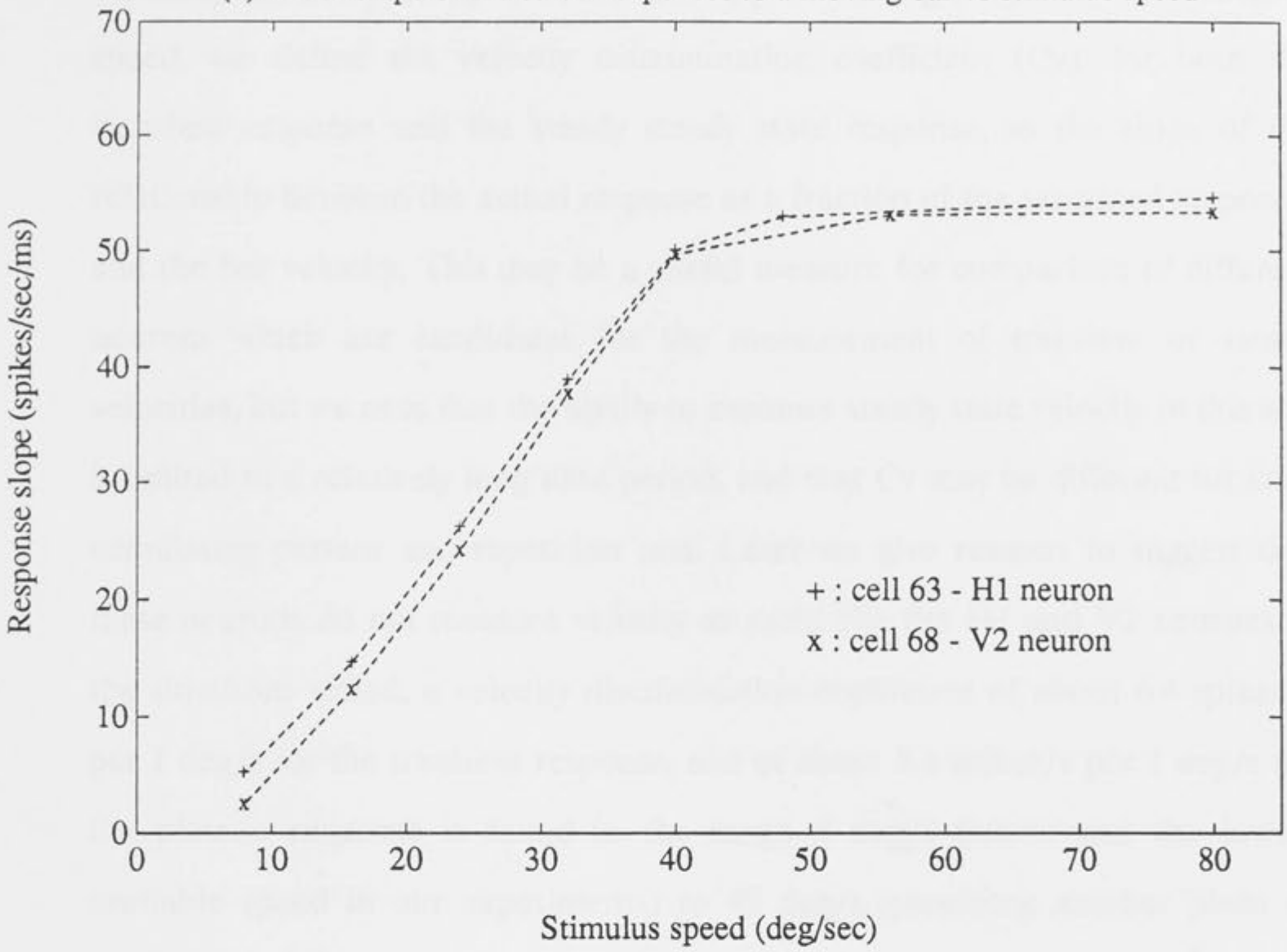
The plateau impulse frequency also depends on the velocity of the bar, for velocities from 8 deg/s, which was the slowest available speed in our experiment, to about 55 deg/s (figure 4-7b). The response saturates above this speed. Once again there is no siginificant difference between H1 and V2, except that the curve for V2 appears to shift to the left, and its plateau response saturates at velocity slightly below 55 deg/s.

Figure 4-7. (a) The transient responses (Rt), (b) the steady state responses, (c) the response slopes of the H1 and V2 neurons, and (d) the time to peak (Tp), versus the bar speed (V). These four parameters together provide a quantitative description of the neuron's response to different speeds. In the experiments with the black bar, the neurons indeed changed these response parameters according to the speed, especially over the range from 8 °/s to about 50 °/s. (a) The transient responses increased monotonically from about 240 spikes/s to 460 spikes/s for cell 63 (a H1 neuron), and from about 180 spikes/s to 425 spikes/s for cell 68 (a V2 neuron). (b) The steady state response also increased from about 150 spikes/s to 270 spikes/s for cell 63, and from about 170 spikes/s to 240 spikes/s for cell 68. The transient and steady state responses of both neurons saturated when the motion was faster than about 50 °/s. (c) The response slope, which was measured as the formula: Rt/(Tp - Tl), where Tl is the latency, also increased linearly from about 4 spikes/s/ms to 50 spikes/s/ms as the speed increased from 8 °/s to about 40 °/s, then saturated. The response slope actually represents the spike firing acceleration, so the neurons indicate the speed increment by just increasing the firing acceleration linearly. (d) The time to peak decreased from an average 80 ms to about 32 ms as the speed increased from 8 °/s to about 50 °/s, which suggests that the response speed increases to fast motions. Note that the responses of H1 and V2 to a moving bar are bigger than to a moving grating (see Fig. 3-8), hinting that the neurons respond better to a single moving object than to a background motion.

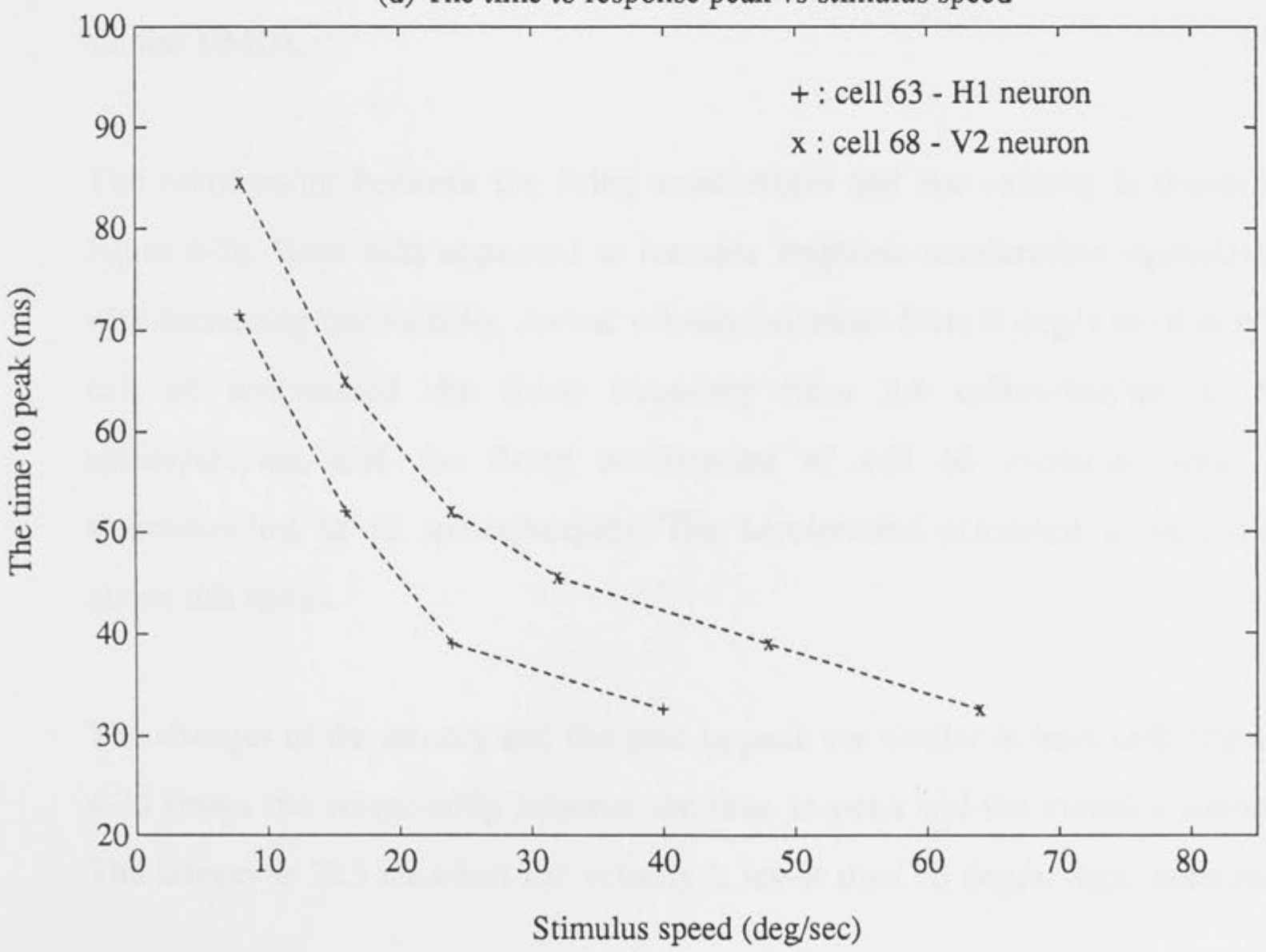

(a) Transient response of H1 & V2 to a moving bar vs stimulus speed
Transient response (spikes/sec)
500
450
400
350
300
250
200
0
10
20
30
40
50
60
70
80
Stimulus speed (deg/sec)
+ : cell 63 - H1 neuron
x : cell 68 - V2 neuron


(b) Steady state response of H1 & V2 to a moving bar vs stimulus speed
Steady state response (spikes/sec)
280
260
240
220
200
180
160
140
0
10
20
30
40
50
60
70
80
Stimulus speed (deg/sec)
+ : cell 63 - H1 neuron
x : cell 68 - V2 neuron

(c) Initial slope of H1 & V2 responses to a moving bar vs stimulus speed



(d) The time to response peak vs stimulus speed



To study the relationship between the response firing frequency and stimulus speed, we define the velocity discrimination coefficient (Cv), for both the transient response and the steady steady state response, as the slope of the relationship between the actual response as a fraction of the saturated response, and the bar velocity. This may be a useful measure for comparison of different neurons which are candidates for the measurement of transient or steady velocities, but we note that the ability to measure steady state velocity in this way is limited to a relatively long time period, and that Cv may be different for each stimulating pattern and repetition rate. Later we give reasons to suggest that these neurons do not measure velocity as such. For the H1 and V2 neurons in the situations tested, a velocity discrimination coefficient of about 6.4 spikes/s per 1 deg/s for the transient response, and of about 3.4 spikes/s per 1 deg/s for the plateau response is found in the range 8 deg/s (which was the lowest available speed in our experiments) to 48 deg/s, providing another piece of evidence that there is no fundamental difference in the processing of horizontal and vertical motion information, and that the inputs of both cells come from similar EMDs.

The relationship between the firing acceleration and bar velocity is shown in figure 4-7c. Both cells appeared to increase response acceleration sigmoidally with increasing bar velocity. As bar velocity increases from 8 deg/s to 48 deg/s, cell 68 accelerated the firing frequency from 2.4 spikes/sec/ms to 52 spikes/sec/ms, and the firing acceleration of cell 63 increased from 8 spikes/sec/ms to 52 spikes/sec/ms. The acceleration saturated at velocities above this speed.

The changes of the latency and the time to peak are similar in both cells (figure 4-7d shows the relationship between the time to peak and the stimulus speed). The latency is 32.5 ms when the velocity is lower than 16 deg/s, then decreases

to 19.5 ms as the speed increases to 32 deg/s, then remains constant. The time to peak decreases progressively from 84.5 ms (cell 68) or 71.5 ms (cell 63) to 32.5 ms, as the velocity increases from 8 deg/s to 48 deg/s (cell 63) or 64 deg/s (cell 68), then keeps constant.

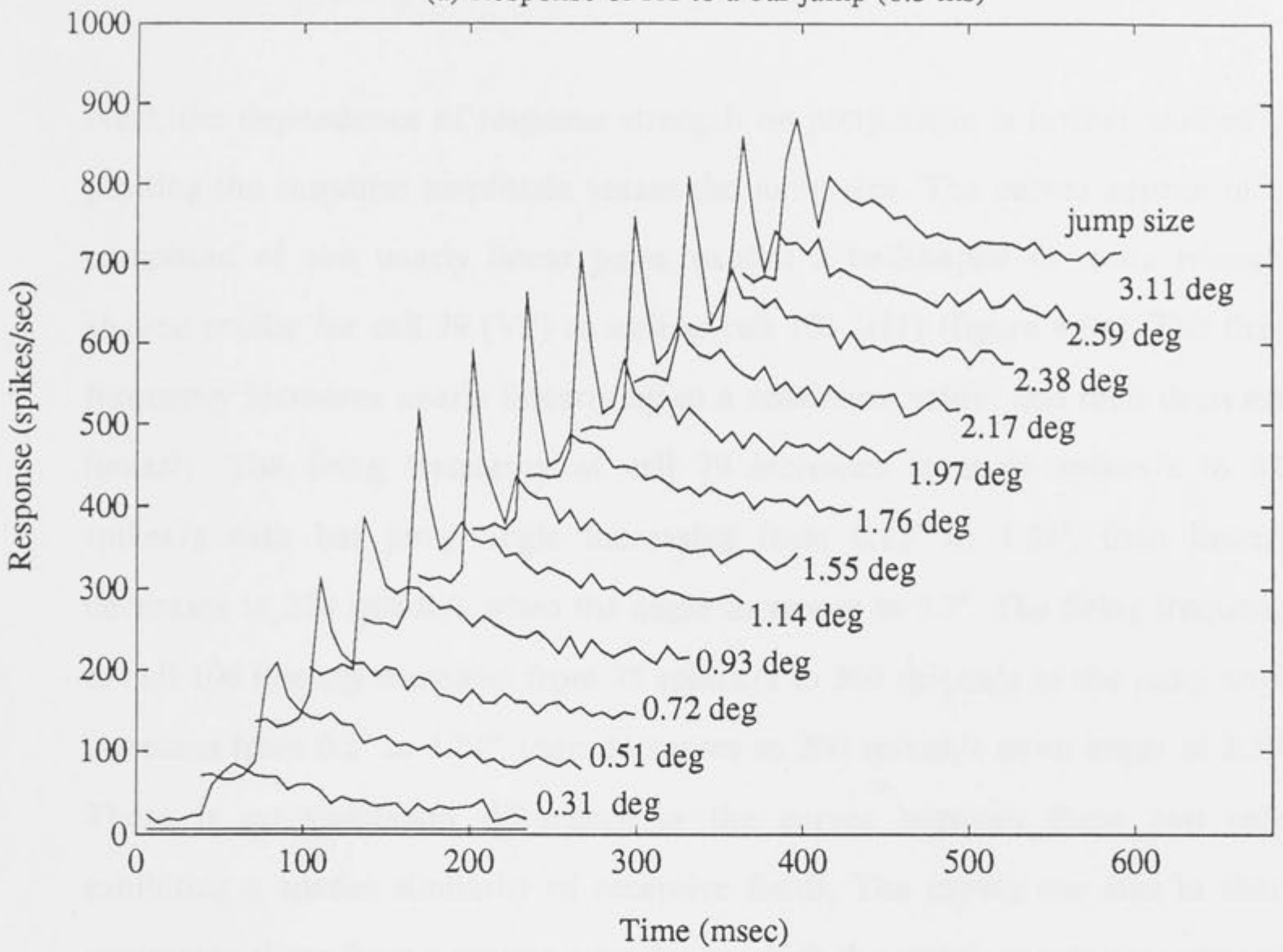
4-3-5. Response to a jump of a bar.

The recordings were made from H1 (cell 69) or V2 (cell 79), with a long dark bar of width 3.32°, jumping through an angle ranging from 0.054 degree to 3.21°. Within this range the differences in response sensitivity in different regions of the eye, produced by afterimages, will be completely eliminated. The duration of the jump was fixed at 1 frame (6.5 ms); the interval between jumps was chosen to be 5 seconds in order to limit temporal influences such as habituation. The responses were averaged over 100 stimulus repetitions.

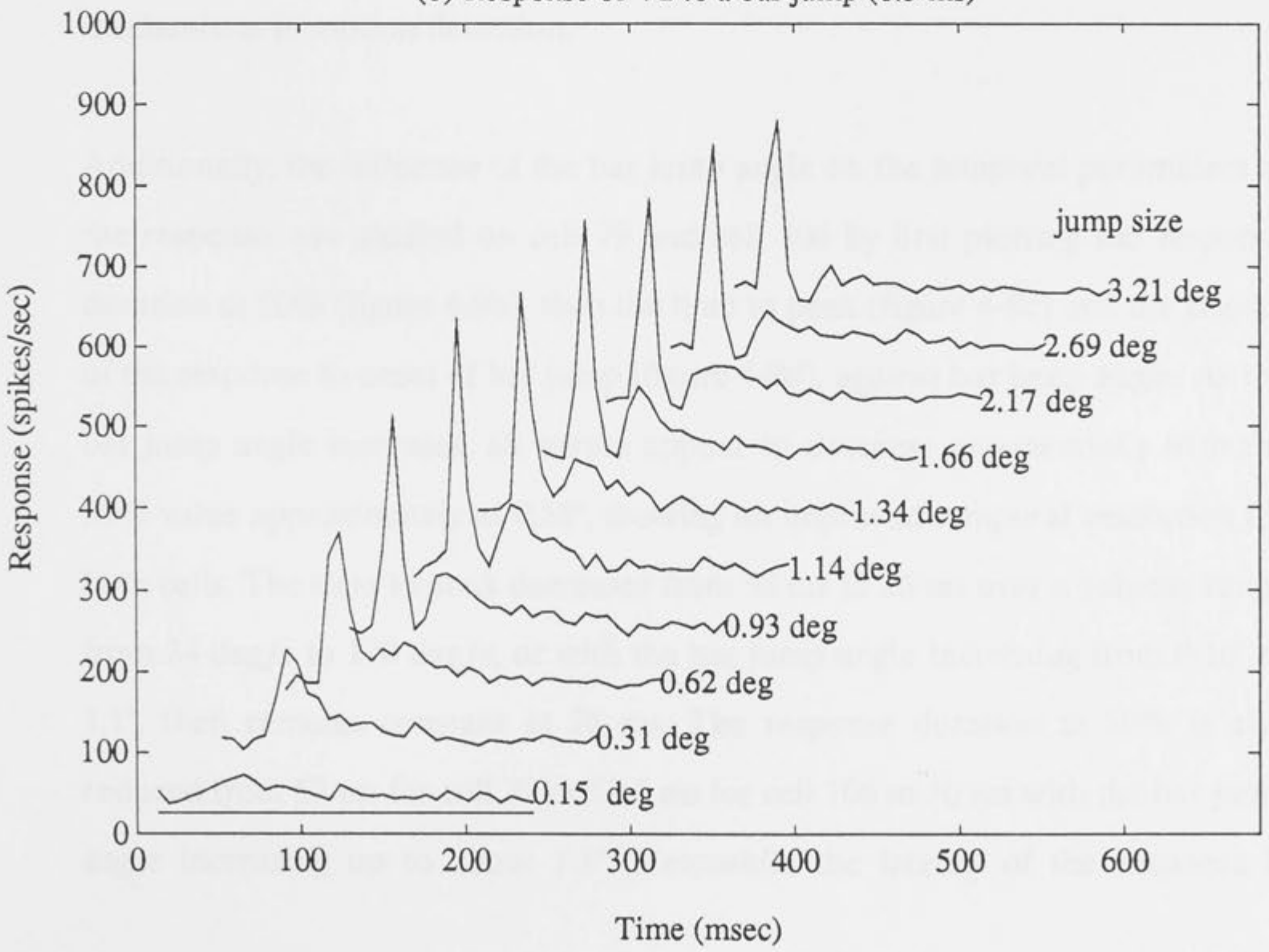
When a dark bar in the visual field of the cells is suddenly jumped to a new location, the response apparently depends on the angular distance jumped. Both cells produced a sharp increase in response amplitude with increasing jump angle, as expected. The firing frequency decayed back to the spontaneous rate after about 180 ms in cell 69 (the H1 neuron) and 120 ms in cell 79 (the V2 neuron). With increasing jump angle, the time to peak decreased from 39 ms to 26 ms for both cells. Unexpectedly, however, when the jump size exceeded a critical value, a second peak appeared at about the half-way-point of the falling phase of the response. The critical jump angle for appearing the second peak was 1.14 degrees for the H1 neuron and 0.62 degrees for the V2 neuron (Fig.4-8).

Figure 4-8. The responses of H1 and V2 to a brief jump (6.5 ms) of a black bar of width 3.3 °. A jump of 6.5 ms obviously falls in the neuron's integration time, so that the response can only reveal the spatial characteristics of the large-field motion-detection, for example the spatial interaction between the EMDs, ignoring the temporal influences. The experiments were carried on both H1 and V2 neurons, the examples of the responses to the jump from 0.15° to 3.21° are shown in (a) for H1 and (b) for V2. As expected, the responses increased as the jump distance increased from 0.15° to about 1°. But surprisingly, the response strength decreased as the jump distance inreased over 1.14°; and even a negative phase as well as a small second peak appeared when the jump distance was larger than about 1°, which is significantly different to the response to a bar continuous movement (see Fig. 4-6a & 4-6b). The widths of the response also decreased as the jump distance increased. These facts suggest a spatial interaction between the EMDs, which inhibits the spike firing. Since the negative phase appeared only about 13 ms after the transient peak, this spatial interaction may have passed through one or two synapses. The stimulus minimum displacement threshold is 0.31° under the experimental condition,

(a) Response of H1 to a bar jump (6.5 ms)



(b) Response of V2 to a bar jump (6.5 ms)



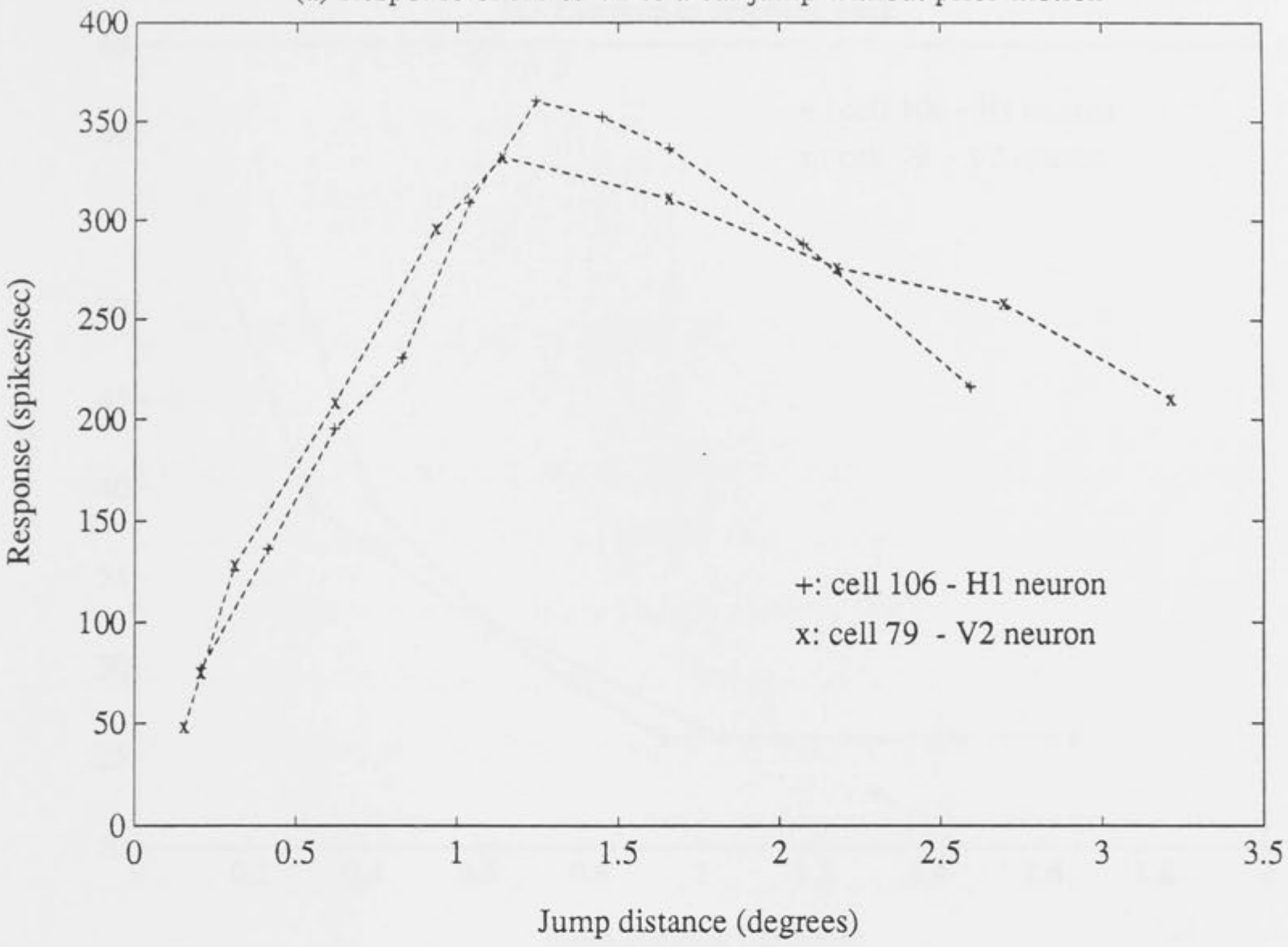
4-3-6. Effects of jump size on response.

Next, the dependence of response strength on jump angle is further studied by plotting the response amplitude versus the jump size. The curves appear to be composed of two nearly linear parts, exhibit a bellshaped or more triangle-shaped profile for cell 79 (V2) as well as cell 106 (H1) (figure 4-9a). The firing frequency increases nearly linearly up to a maximum value, and then decreases linearly. The firing frequency of cell 79 increases from 46 spikes/s to 343 spikes/s with bar jump angle increasing from 0.15° to 1.14°, then linearly decreases to 220 spikes/s when the angle increases to 3.2°. The firing frequency of cell 106 linearly increases from 75 spikes/s to 360 spikes/s as the jump angle increases from 0.2° to 1.24°, then decreases to 260 spikes/s at an angle of 2.59°. There is no significant difference in the curves between these two cells, exhibiting a spatial similarity of receptive fields. The curves are also in sharp contrast to those from a grating stimulus in which the transient response virtually never drops down (Fig.3-8), suggesting that there might be two kinds of mechanisms in motion detection.

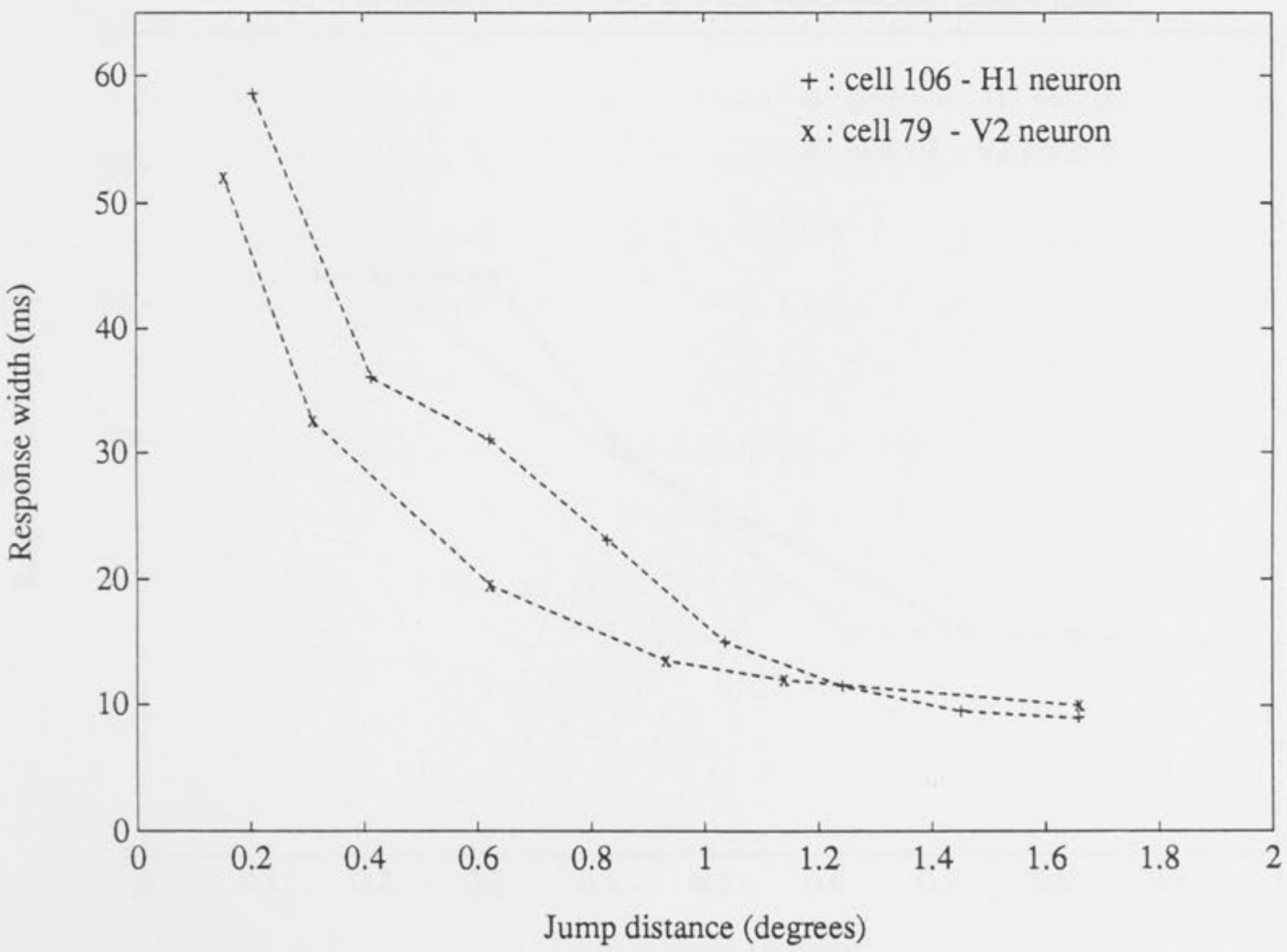
Additionally, the influence of the bar jump angle on the temporal parameters of the response was studied on cell 79 and cell 106 by first plotting the response duration at 50% (figure 4-9b), then the time to peak (figure 4-9c) and the latency of the response to onset of bar jump (figure 4-9d), against bar jump angle. As the bar jump angle increases, all curves appear to decrease exponentially with the 50% value approximately at 0.56°, showing an improved temporal resolution for both cells. The time to peak decreases from 58 ms to 26 ms over a velocity range from 24 deg/s to 170 deg/s, or with the bar jump angle increasing from 0.16° to 1.1°, then remains constant at 26 ms. The response duration at 50% is also reduced from 52 ms for cell 79 or 58.5 ms for cell 106 to 10 ms with the bar jump angle increasing up to about 1.4°. Meanwhile the latency of the response is

Figure 4-9. The response strength (a), width (b), latency (c) and the time to peak (d) of a H1 and V2 neurons plotted versus a black bar brief jump distance without prior-motion. The transient response of both neurons increased almost linearly from 50 spikes/s to about 350 spikes/s as the jump angular distance increased from about 0.15° to 1.25°, confirming again that the response height is linearly dependent on the displacement during the integration time. It decreased to about 200 spikes/s when the jump angle was over about 3° (a). The ratio of the response acceleration to the jump distance is approximately 270 spikes/s/degree, which obviously is larger than the response to a moving grating (Fig. 3-8). Actually, the response of H1 appears to be slightly stronger than the response of V2, especially at the maximum value. The V2 neuron was usually more faster than the H1, possessing shorter time constants, in terms of the width (b) and the time to peak (c); although the both kinds of temporal parameters of H1 and V2 eventually declined exponentially to a same ultimate value, about 10 ms for the width and 26 ms for the time to peak. However, both neurons had the same latency 26 ms in response to a bar jump from 0.15° to about 0.3°, which decreased to 13 ms when the jump angle was over 0.61° (c).

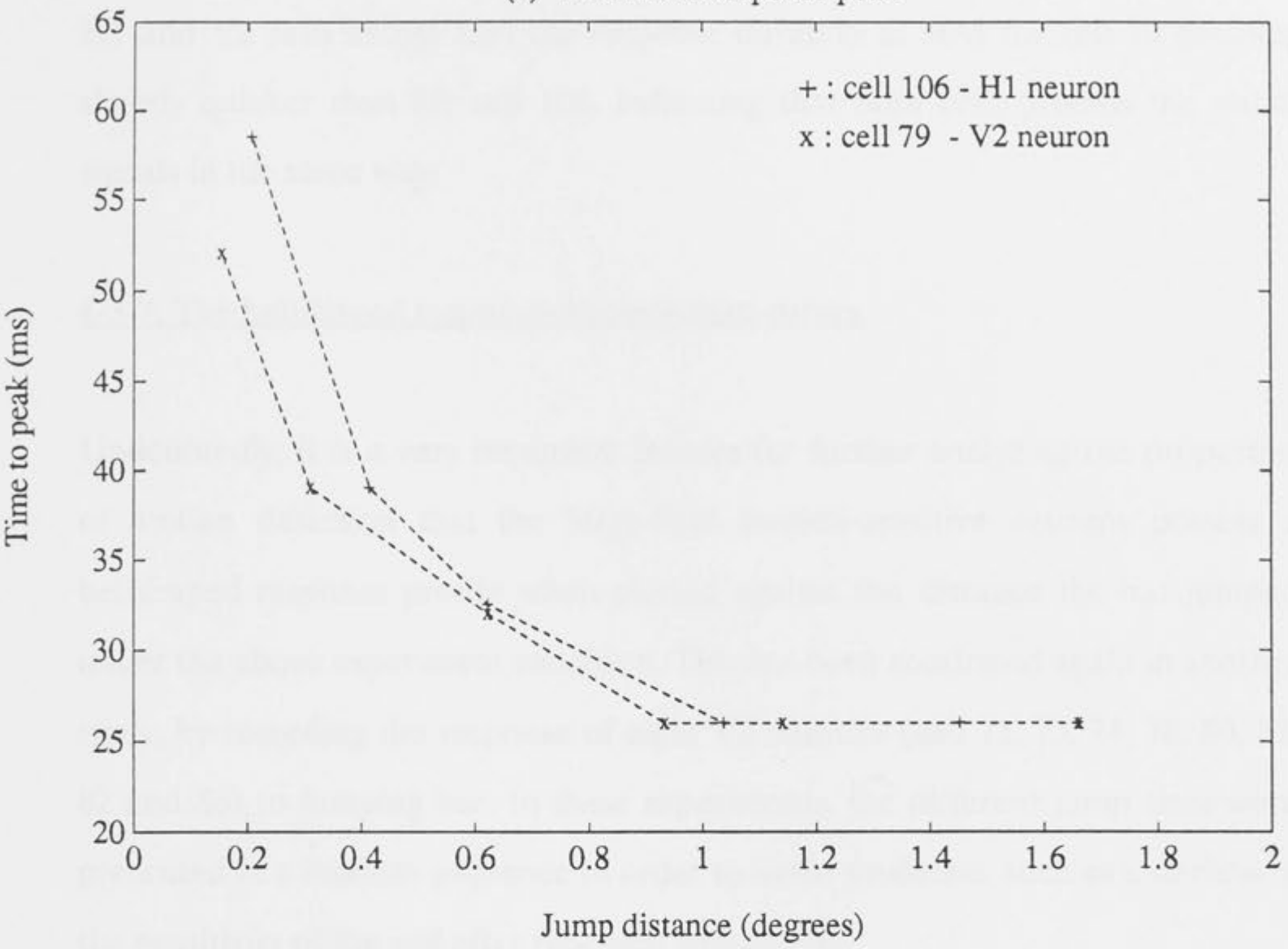
(a) Response of H1 & V2 to a bar jump without prior-motion



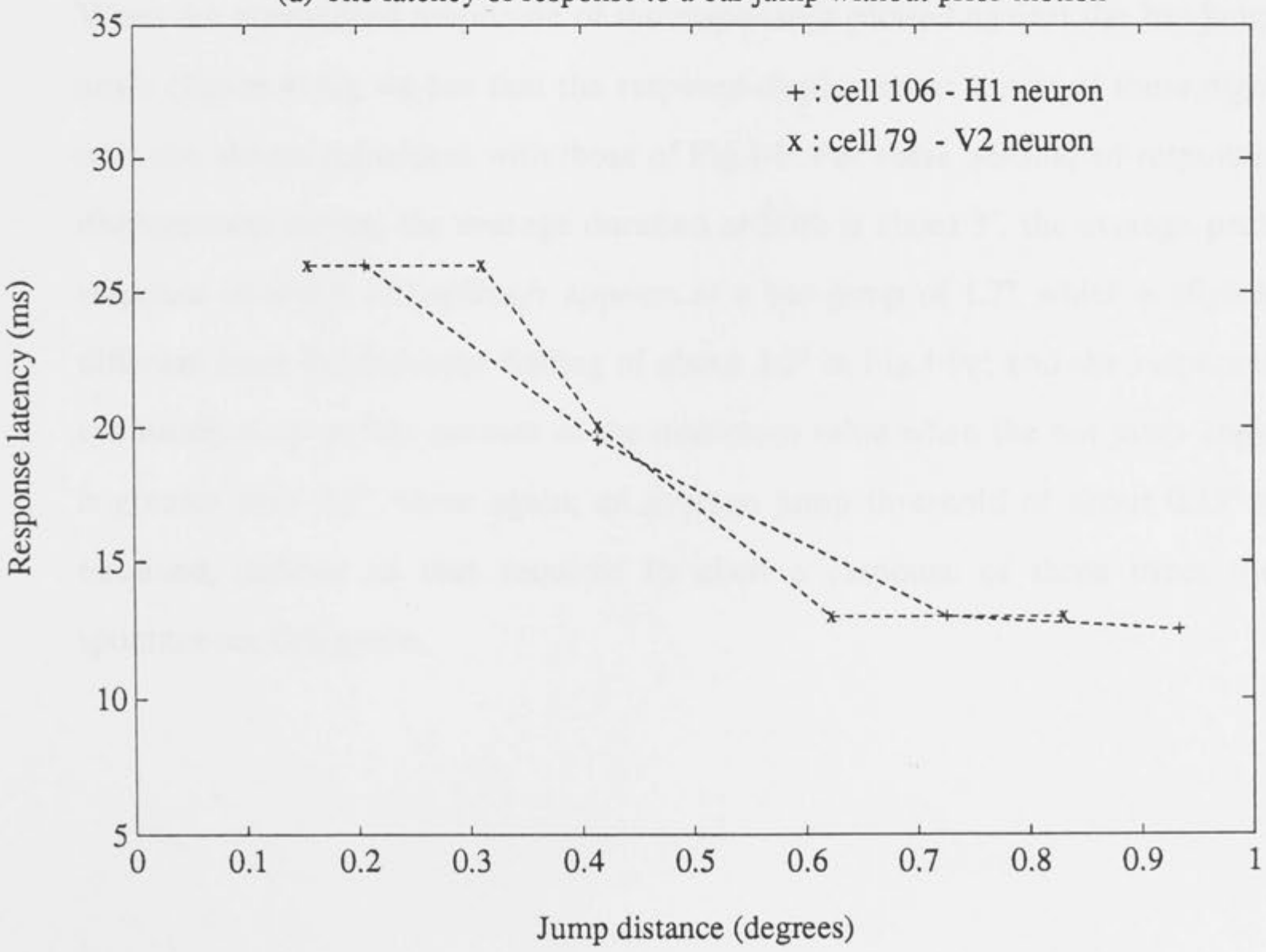
(b) The width of response to a bar brief jump (6.5 ms)



(c) The time to response peak



(d) The latency of response to a bar jump without prior-motion



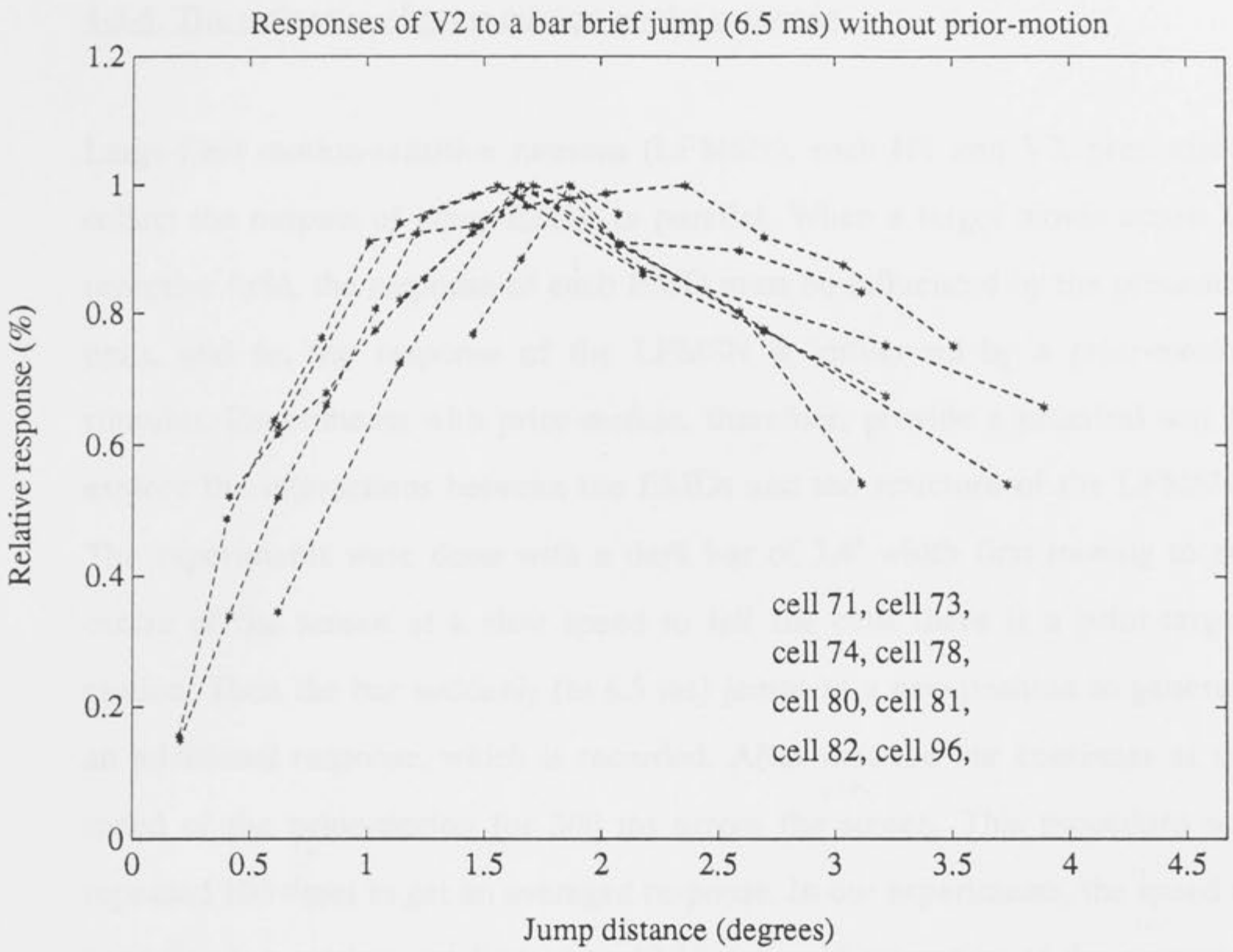
reduced from 26 ms to 13 ms. No significant difference was observed between H1 and V2 cells except that the response duration at 50% for cell 79 declines slightly quicker than for cell 106, indicating that both cells process the visual signals in the same way.

4-3-7. The bellshaped response-displacement curves.

Undoubtedly, it is a very important feature for further analyzing the properties of motion detection that the large-field motion-sensitive neurons possess a bellshaped response profile when plotted against the distance the bar jumped under the above experiment condition. This has been confirmed again in another study, by recording the response of eight V2 neurons (cell 71, 73, 74, 78, 80, 81, 82 and 86) to jumping bar. In these experiments, the different jump sizes were presented in a random sequence in order to avoid problems, such as a decline in the sensitivity of the cell after repeated stimulation.

When the normalized amplitude of the response is plotted against the bar jump angle (figure 4-10), we see that the response-displacement curves of these eight cells are almost coincident with those of Fig.4-9. For these bellshaped response-displacement curves, the average duration at 50% is about 3°. the average peak response of about 270 spikes/s appears at a bar jump of 1.7°, which is slightly different from the previous finding of about 1.2° in Fig.4-9a; and the responses eventually drop to fifty percent of the maximum value when the bar jump angle is greater than 3.7°. Once again, an average jump threshold of about 0.13° is obtained, defined as that required to elicit a response of three times the spontaneous firing rate.

Figure 4-10. Demonstration of a large-field motion-detector possessing a bellshaped response-displacement curve. The experiments were done on eight V2 neurons, which responded to brief jumps varied from .15° to 3.8° without prior-motion, of a black bar of width 3.3°. The peak of the curves is at about 1.7°, the width is about 3.5° at the half of the peak. This phenomenon is in sharp contrast to the responses to a moving bar or grating, which remained at a high level a high level after the distance moved was larger than 1.7° (Fig. 4-3 and Fig. 3-8). The bellshaped response-displacement curve must reflect the spatial properties of motion detection locally, showing that the EMDs possess a limited receptive field.


Responses of V2 to a bar brief jump (6.5 ms) without prior-motion
Relative response (%)
1.2
1
0.8
0.6
0.4
0.2
0
0
0.5
1
1.5
2
2.5
3
3.5
4
4.5
cell 71, cell 73,
cell 74, cell 78,
cell 80, cell 81,
cell 82, cell 96,
Jump distance (degrees)

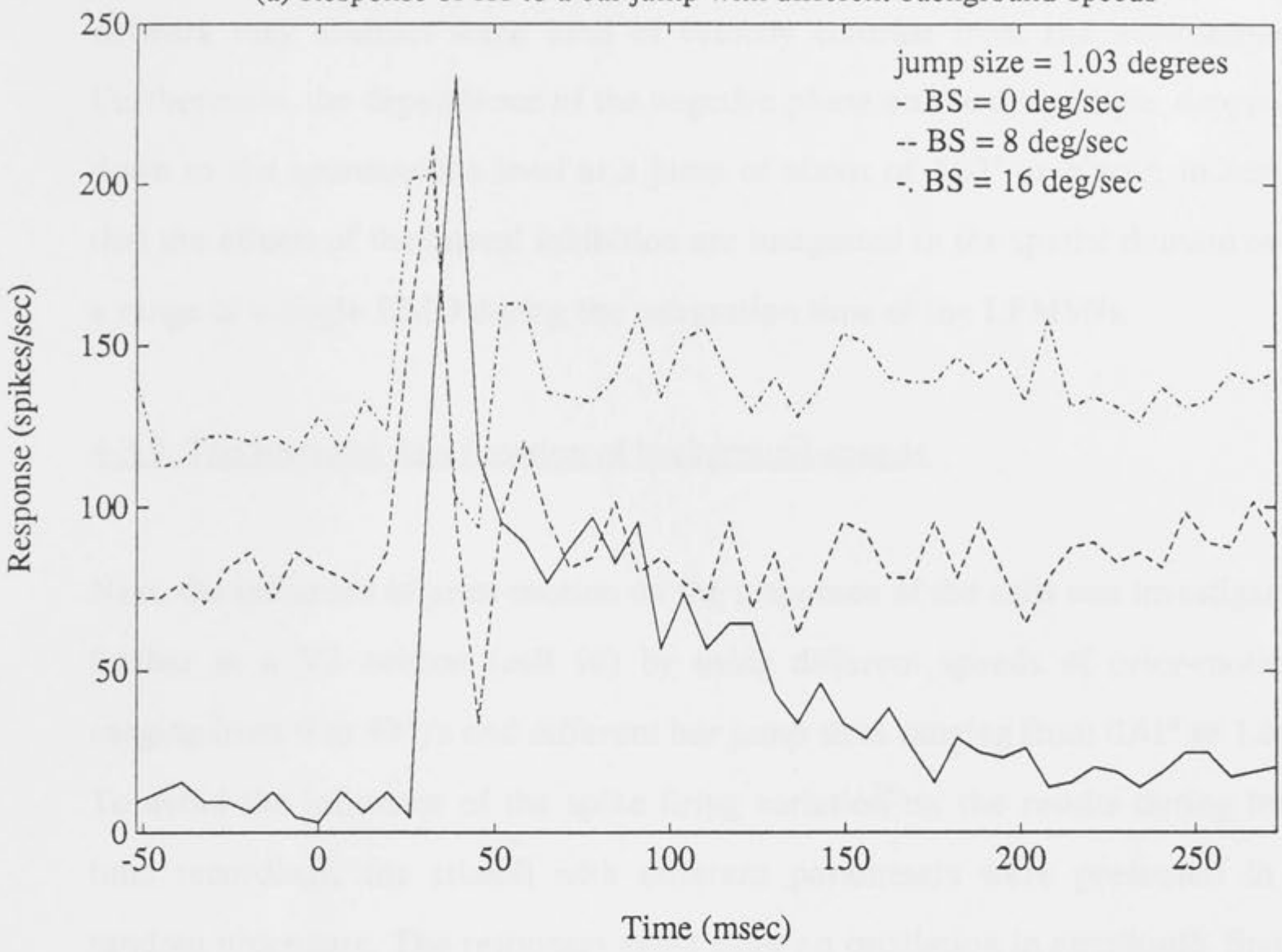
4-3-8. The influence of prior motion on the response.

Large-field motion-sensitive neurons (LFMSN), such H1 and V2, presumably collect the outputs of many EMDs in parallel. When a target moves across its receptive field, the response of each EMD must be influenced by the preceding units, and so, the response of the LFMSN is influenced by a prior-motion stimulus. Experiments with prior-motion, therefore, provide a practical way to explore the interactions between the EMDs and the structure of the LFMSNs. The experiments were done with a dark bar of 3.4° width first moving to the centre of the screen at a slow speed to tell the cells there is a prior-target-motion. Then the bar suddenly (in 6.5 ms) jumps to a new position to generate an additional response, which is recorded. After that the bar continues at the speed of the prior-motion for 300 ms across the screen. This procedure was repeated 100 times to get an averaged response. In our experiments, the speed of bar prior bar motion was limited to 40 °/s to avoid saturation of the response; and the jump angle was varied from 0.2° to 3.4° which means that it may reveal interactions between neighbouring EMDs.

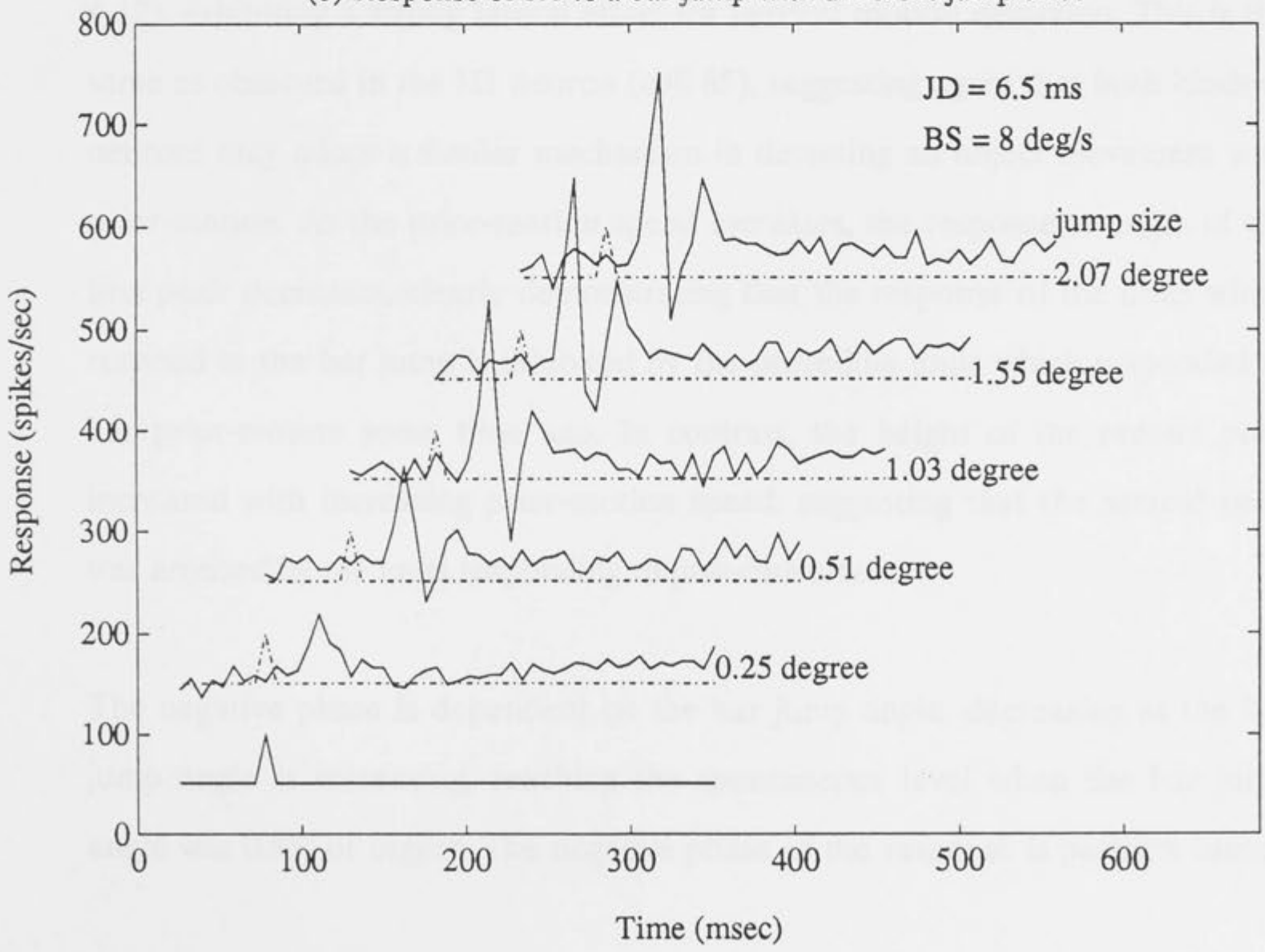
An example of the responses of H1 neuron, recorded from cell 85 with prior bar motion of 8 °/s and jump angle ranging from 0.27° to 2.7°, is shown in figure 4-11. Compared to the response without prior-motion stimulus (for example cell 69 in Fig.4-8a), the responses of cell 85 exhibit an interesting feature in that the firing frequency appears to oscillate in amplitude with time. Surpringly, the first peak is immediately followed by a non-response phase (Fig.4-11) properly called a negative or inhibitory phase that becomes stronger with increasing bar jump angle, which is obviously different from that without prior-motion. The fact that the transient response with prior-motion was smaller than without prior-motion and that a negative phase appeared after the jump distance was larger than 1.03°, suggests again that there is a local instantaneous spatial lateral interaction

Figure 4-11. The influence of background speeds on the response of H1. Background speed is defined as the speed of a bar which is moving at a constant speed before and after the bar briefly jumps. In the experiment, the background speeds were 0 °/s (i.e, without prior-motion), 8 °/s and 16 °/s, the bar jump angular distance is varied from 0.25° to 2.07°. (a) As the background speed increased, the transient response decreased and a negative phase appeared; the latency and especially the time to peak also became shorter. (b) With the same background speed but different jump distances, the negative phase appeared only after the jump distance was larger than 1.03°. Secondly, the transient peak as well as a small second peak always increased as the jump distance increased. The shorter time constants (such as, the time to peak and the latency) when there is prior-motion, indicates that the neuron responds faster to a moving object which suddenly changes its speed than to the take-off from stationary state.

(a) Response of H1 to a bar jump with different background-speeds



(b) Response of H1 to a bar jump with different jump sizes



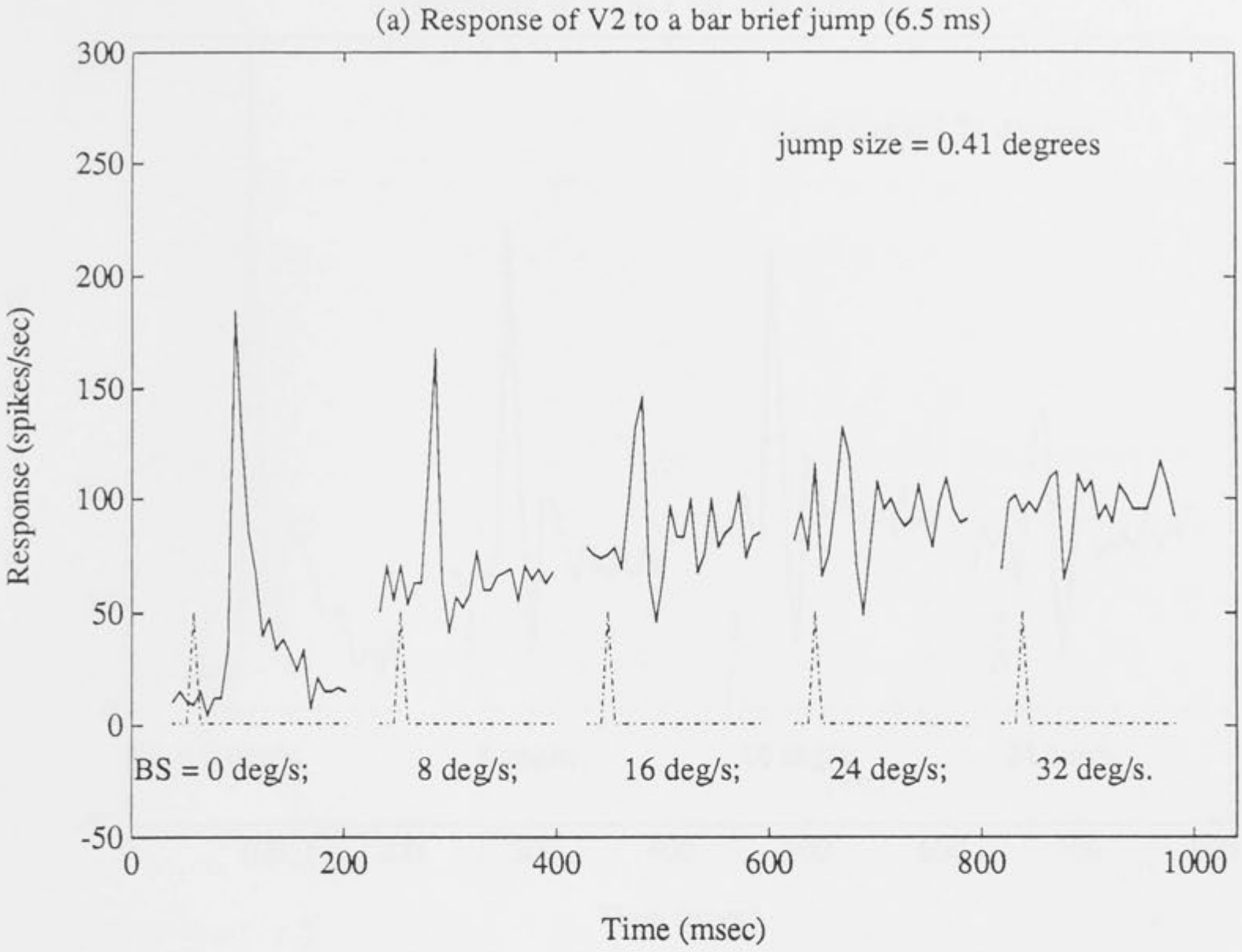
between the EMDs. Functionally, the EMDs units with a lateral inhibition network may abstract some kind of velocity contrast from the environment. Furthermore, the dependence of the negative phase on the jump angle, dropping down to the spontaneous level at a jump of about of 1.03° or bigger, indicates that the affects of the lateral inhibition are integrated in the spatial domain over a range of a single EMD during the integration time of the LFMSNs.

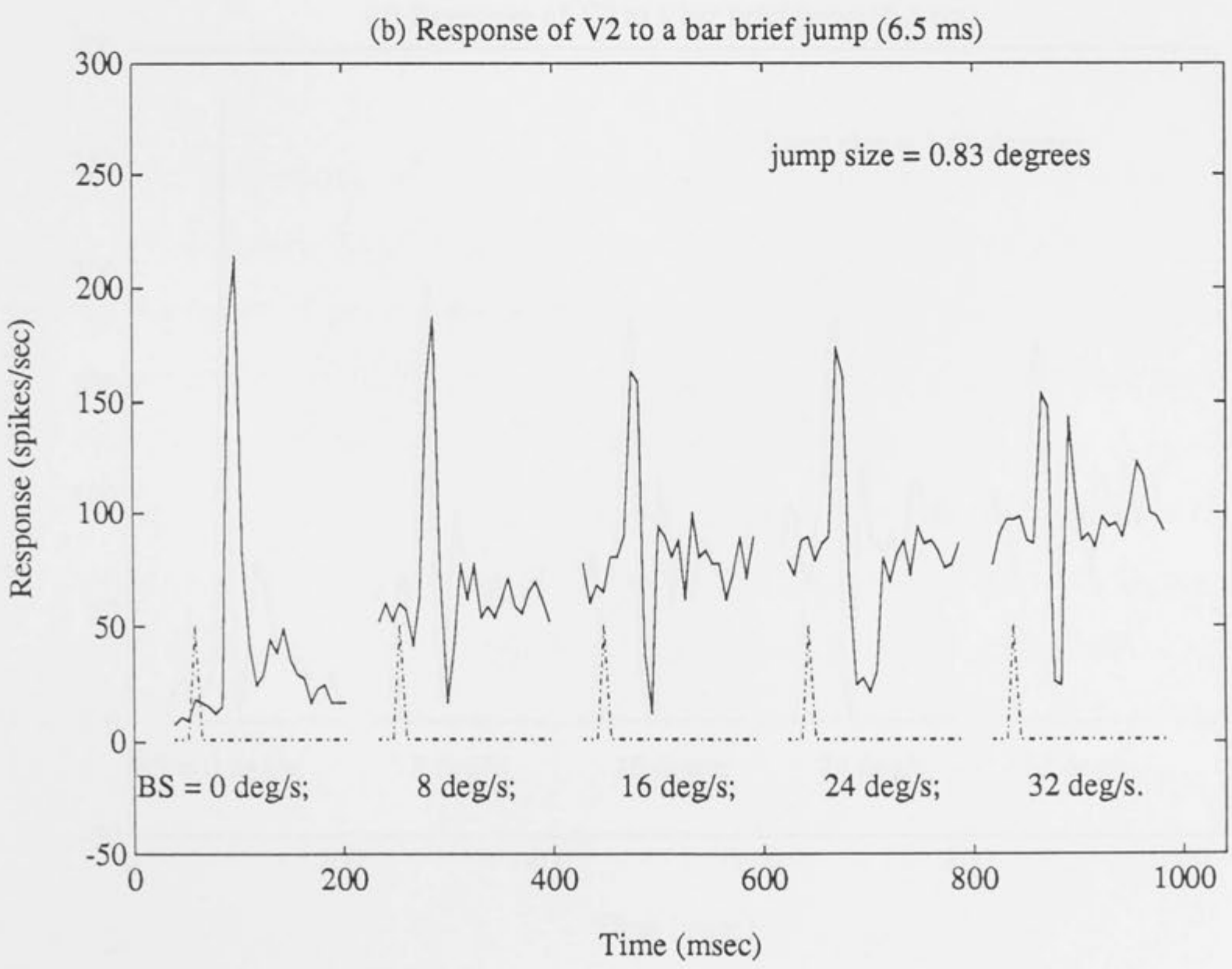
4-3-9. The response as a function of background-speeds.

Next, the influence of prior-motion on the responses of the cells was investigated further in a V2 neuron (cell 90) by using different speeds of prior-motion, ranging from 0 to 40 °/s and different bar jump sizes ranging from 0.41° to 1.66°. To avoid the influence of the spike firing variation on the results during long time recordings, the stimuli with different parameters were presented in a random procedure. The responses again show an oscillation in amplitude, first a big response peak then strong negative phase then a smaller second peak (figure 4-12), exhibiting a strong lateral effect for vertical motion detection. This is the same as observed in the H1 neuron (cell 85), suggesting again that both kinds of neurons may adopt a similar mechanism in detecting an object movement with prior-motion. As the prior-motion speed increases, the response strength of the first peak decreases, clearly demonstrating that the response of the units which respond to the bar jump is inhibited by the preceding units which responded to bar prior-motion some time ago. In contrast, the height of the second peak increased with increasing prior-motion speed, suggesting that the second peak was aroused by the units responding to post-movement.

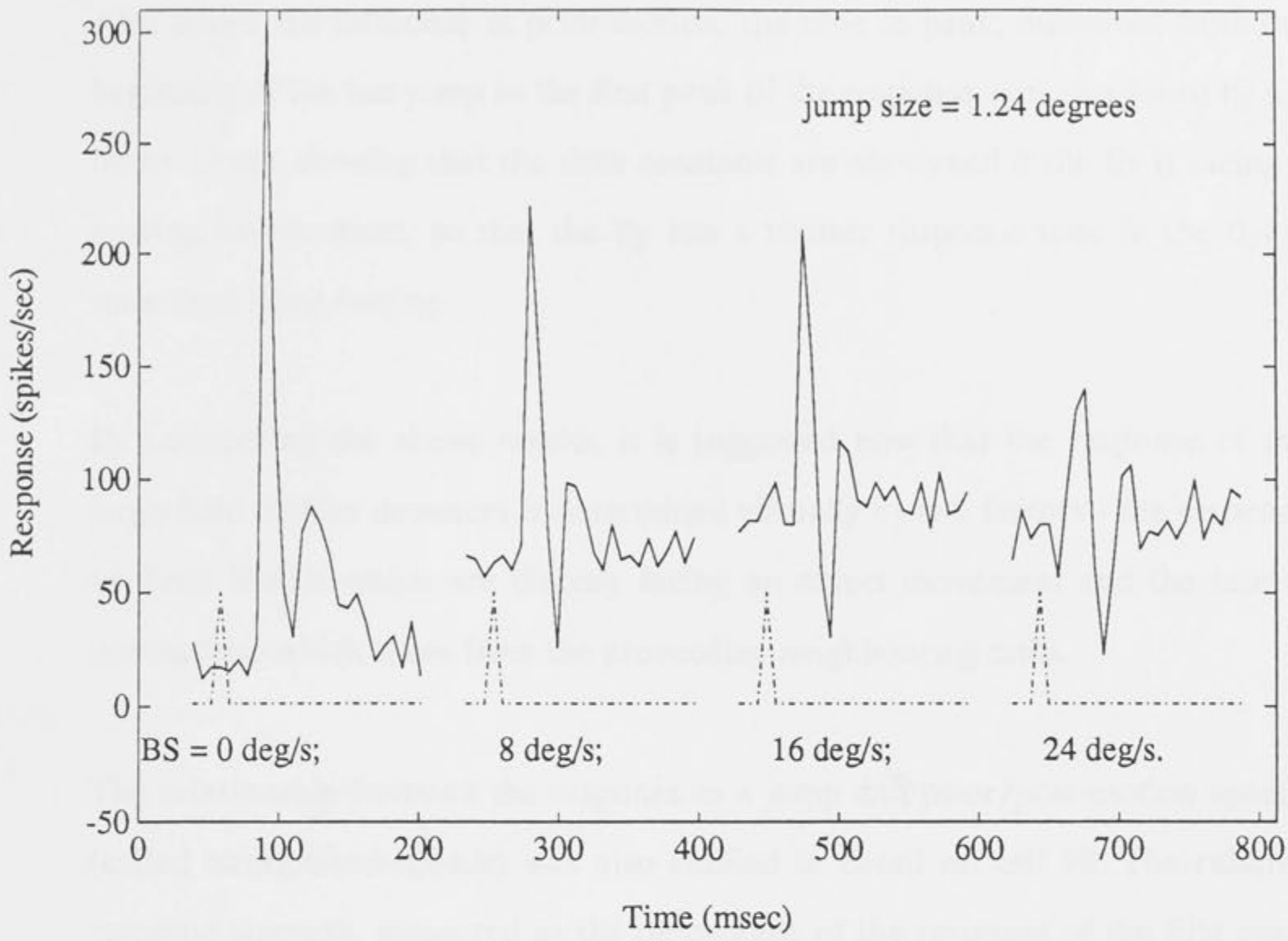
The negative phase is dependent on the bar jump angle, decreasing as the bar jump angle is increasing, reaching the spontaneous level when the bar jump angle was 0.83° or bigger. The negative phase of the response is perhaps caused

Figure 4-12. The responses of a V2 neuron to brief jumps of a black bar with different background speeds as indicated. Jump distances ranged from 0.41° to 1.66° and the background speed was at 0 °/s, 8 °/s, 16 °/s, 24 °/s and 32 °/s. As the background speed increased, the transient response decreased, as in the H1 neuron (Fig. 4-11), and even disappeared in the case of jumping larger than 0.41° with prior-motion 32 °/s. A clear negative phase appeared when the jump distance was larger than 0.41° and the background speed was greater than 16 °/s; it became stronger as the jump distance increased, showing lateral effects of background motion.

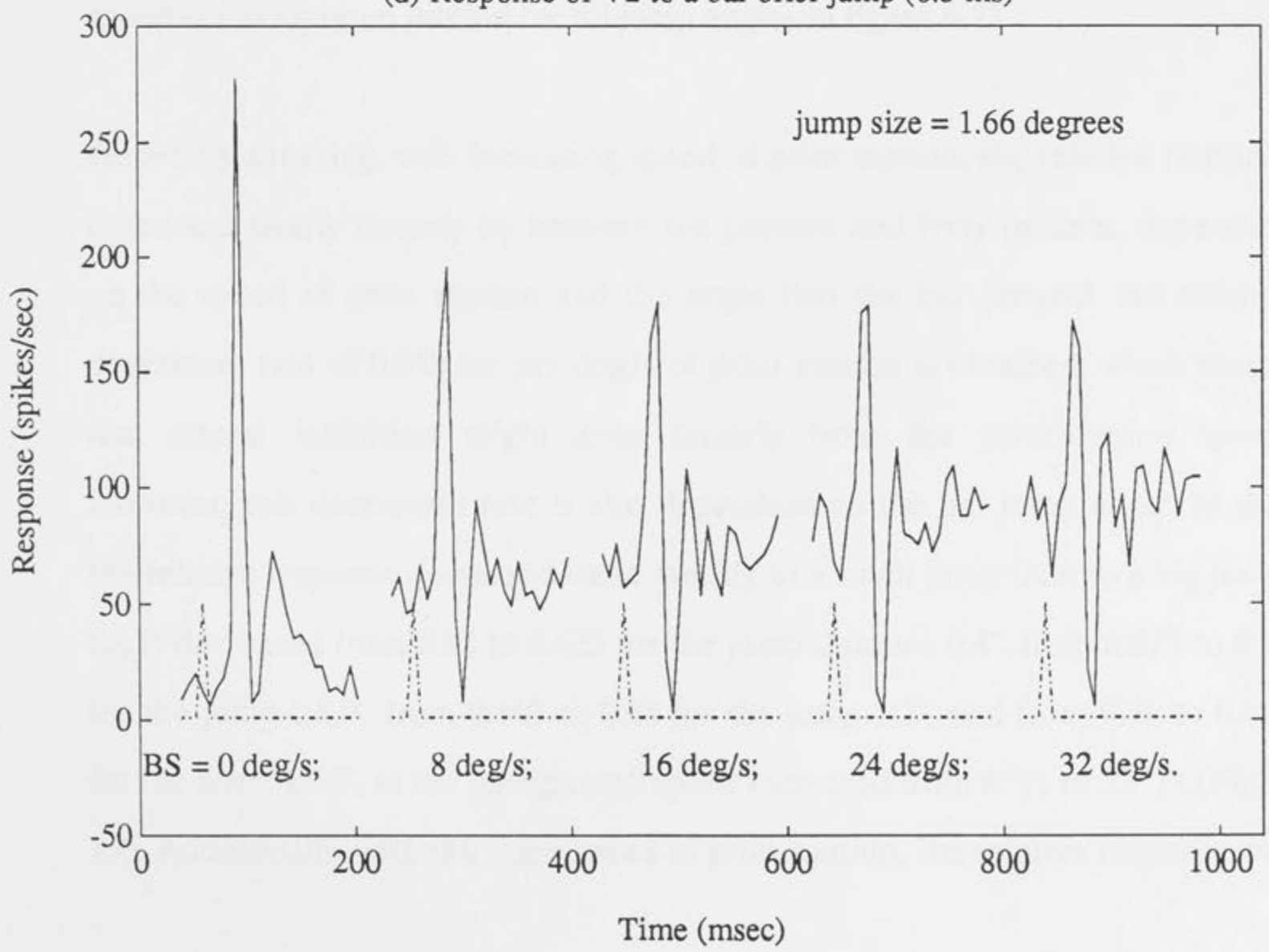

(a) Response of V2 to a bar brief jump (6.5 ms)
jump size = 0.41 degrees
Response (spikes/sec)
Time (msec)
BS = 0 deg/s;
8 deg/s;
16 deg/s;
24 deg/s;
32 deg/s.
300
250
200
150
100
50
0
-50
0
200
400
600
800
1000


(b) Response of V2 to a bar brief jump (6.5 ms)
jump size = 0.83 degrees
Response (spikes/sec)
Time (msec)
BS = 0 deg/s;
8 deg/s;
16 deg/s;
24 deg/s;
32 deg/s.
300
250
200
150
100
50
0
-50
0
200
400
600
800
1000

(c) Response of V2 to a bar brief jump (6.5 ms)



(d) Response of V2 to a bar brief jump (6.5 ms)



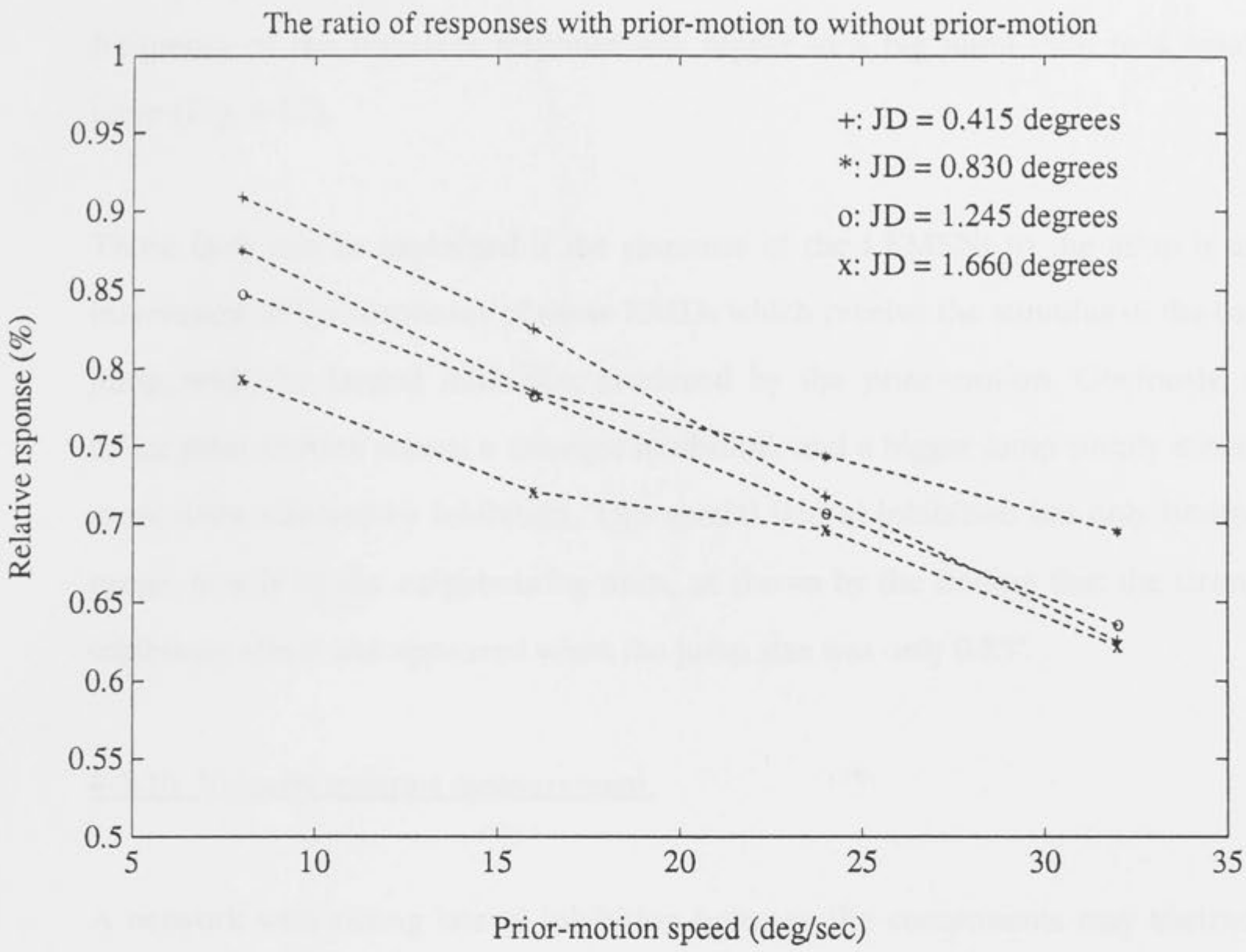
by the lateral inhibition acting on units which are responding to the bar jump. Also under the influence of prior-motion, the time to peak, measured from the beginning of the bar jump to the first peak of the response, was shortened by 6.5 ms to 13 ms, showing that the time constants are shortened if the fly is facing a moving environment, so that the fly has a shorter response time in the flying state than when resting.

By considering the above results, it is suggested now that the response of the large-field motion detectors is determined virtually by two factors - the response of those EMDs which are directly facing an object movement and the lateral interactions which come from the proceeding neighbouring units.

The relationship between the response to a jump and prior/post-motion speeds (called background-speeds) was also studied in detail on cell 90. The relative response strength, measured as the percentage of the response of the first peak with prior-motion to the response without prior-motion, was plotted against the speed of background motion for all jump angles in figure 4-13.

Generally speaking, with increasing speed of prior motion, the relative response decreased nearly linearly by between ten percent and forty percent, depending on the speed of prior motion and the angle that the bar jumped. An average decrement rate of 0.8% for per deg/s of prior motion is obtained, which means that lateral inhibition might arise linearly from the prior-motion speed. However, this decrement rate is also dependent on the bar jump angle, as that the relative response decreased more quickly to a small jump than to a big jump, i.e, it decreased from 0.92 to 0.625 for the jump distance 0.4°, from 0.875 to 0.74 for the jump 0.83°, from 0.845 to 0.68 for the jump 1.2°, and from 0.79 to 0.624 for the jump 1.66°, as the background speed increased from 8 °/s to 32 °/s (Fig.4-13). Additionally, with the same speed of prior motion, the relative response was

Figure 4-13. A comprehensive measurement of the influence of the prior-motion on the response. The relative response is plotted as the ratio of the transient response at prior-motion speed 0 °/s to the transient response under the influence of the prior-motion, against the prior-motion speed. Two tendencies are revealed: first, as the prior-motion speed increased, the relative response decreased approximately linearly, and more quickly to a smaller jump than to a bigger jump. An average rate of 0.8% per deg/s of prior motion is obtained. Secondly, in most cases the relative response to a small jump was stronger than that to a big jump, although the neuron actually produced a stronger absolute response to a big jump.


The ratio of responses with prior-motion to without prior-motion
+: JD = 0.415 degrees
*: JD = 0.830 degrees
o: JD = 1.245 degrees
x: JD = 1.660 degrees
Relative rsponse (%)
1
0.95
0.9
0.85
0.8
0.75
0.7
0.65
0.6
0.55
0.5
5
10
15
20
25
30
35
Prior-motion speed (deg/sec)

usually bigger to a small jump than to a big jump, although the absolute firing frequency of the transient response was bigger to a big jump than to a small jump (Fig. 4-12).

Those facts can be explained if the response of the LFMSNs to the jump is an interaction of the responses of those EMDs which receive the stimulus of the bar jump, with the lateral inhibition produced by the prior-motion. Obviously, a faster prior-motion means a stronger inhibition, and a bigger jump simply means more units affected by inhibition. This spatial lateral inhibition has only limited range, mostly by the neighbouring units, as shown by the finding that the strong inhibitory effect was appeared when the jump size was only 0.83°.

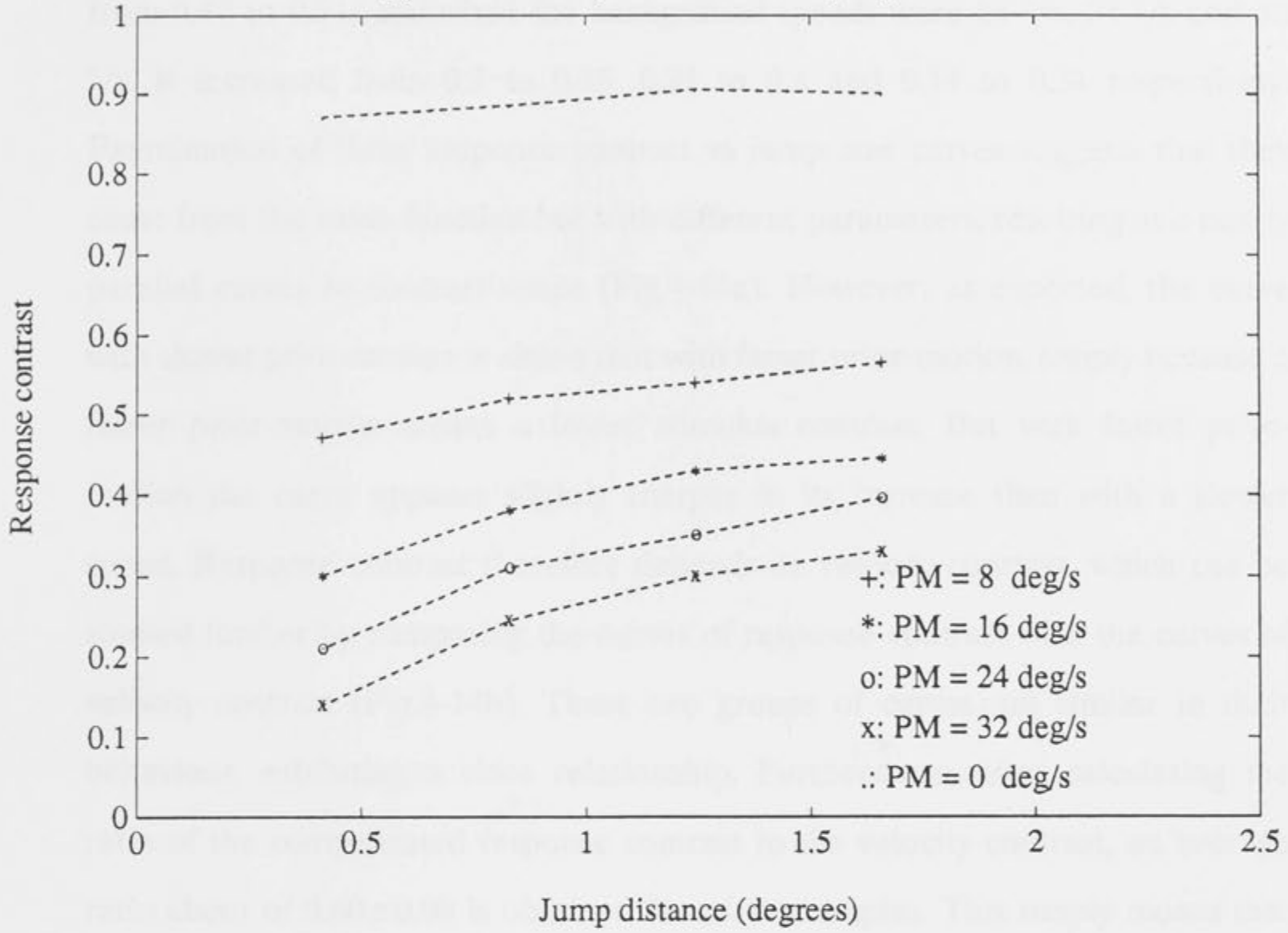
4-3-10. Velocity contrast measurement.

A network with strong lateral inhibition between the components may abstract some kind of contrast in the stimulus; in this case measuring the velocity contrast in the movement. So let us now look at this kind of measurement, by studying the response contrast as a function of jump angle or jump velocity, and then relate this to the velocity contrast of bar movement. The response contrast is measured by dividing the firing frequency of the peak transient response by the mean firing frequency of the response to the prior-motion. The velocity of the bar jump is defined as the ratio of jump angle to jump duration (6.5 ms). The velocity contrast is defined as the ratio of the speed of the jump to the speed of the prior motion.

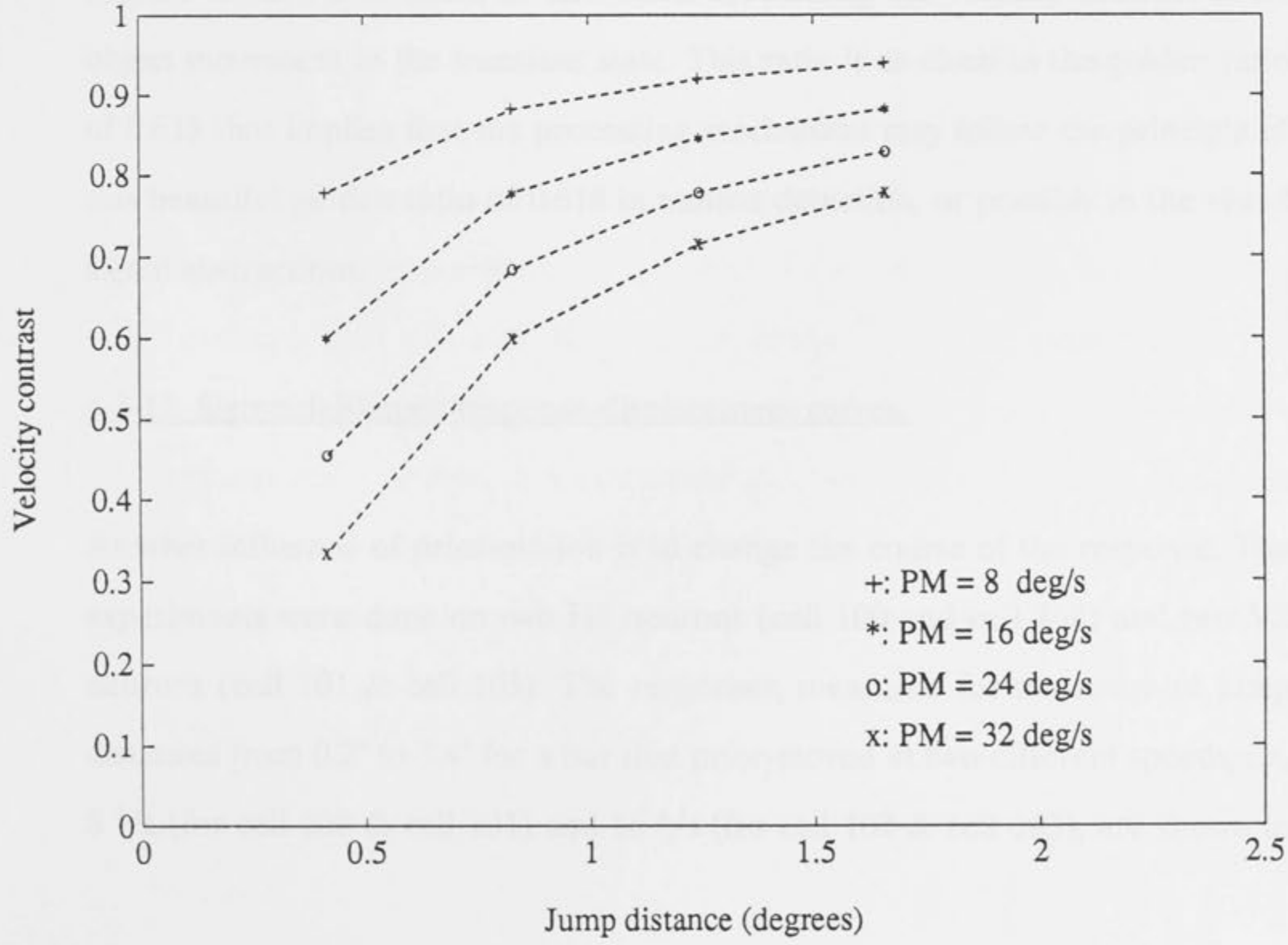
As velocity contrast is increased, by increasing the bar jump angle, the response contrast follows linearly (figure 4-14a). With increasing the bar jump angle from 0.415° to 1.66°, the contrast of the response increased in the following way: when the background speed of bar movement was 0 °/s the response contrast

Figure 4-14. The transient response contrast as a function of jump angle. The transient response contrast is measured by dividing the peak firing frequency of the transient response to the bar jump, by the mean firing frequency of the response to the bar prior-motion. The transient velocity contrast of a bar jump is defined as a ratio of the bar jump speed to the background speed of the bar motion. The speed of the bar jump is measured by dividing the jump angular distance by the jump duration (6.5 ms). As the jump angle increased from 0.415° to 1.66° in 0.415° steps, which also means increasing velocity contrast, the transient response contrast also increased, and all response contrast curves appear to be a linear function of the transient velocity contrast. This is demonstrated by comparing the response contrast curves with the velocity contrast curves (in (b)), which shows that both kinds of curves have a similar shape when plotted against the jump distance. In fact, after making a quantitative calculation about the ratio of the compensated transient response contrast to the transient velocity contrast, an average ratio of 0.6±0.08 is obtained, suggesting that there is a velocity contrast measurement in motion detection (see also in Fig 5-12).

(a) Transient response contrast vs jump distance



(b) Velocity contrast vs jump distance



increased from 0.87 to 0.9; when the background speed was 8 °/s it increased from 0.47 to 0.51; and when the background speeds were 16 °/s, 24 °/s and 32 °/s, it increased from 0.3 to 0.45, 0.21 to 0.4 and 0.14 to 0.34 respectively. Examination of these response contrast vs jump size curves suggests that they come from the same function but with different parameters, resulting in a nearly parallel curves in contrast space (Fig.4-14a). However, as expected, the curve with slower prior-motion is above that with faster prior-motion, simply because a faster prior-motion means a lower stimulus contrast. But with faster prior-motion the curve appears slightly sharper in its increase than with a slower speed. Response contrast therefore depends on velocity contrast, which can be studied further by comparing the curves of response contrast with the curves of velocity contrast (Fig.4-14b). These two groups of curves are similar in their behaviour, exhibiting a close relationship. Furthermore, after calculating the ratio of the compensated response contrast to the velocity contrast, an average ratio about of 0.60 ± 0.08 is obtained for most examples. This simply means that the ratio of the transient response contrast to velocity contrast of the LFMSNs may be around a constant at 0.60 when abstracting the velocity contrast of an object movement in the transient state. This ratio is so close to the golden ratio of 0.618 that implies that the processing mechanism may follow the principle of this beautiful golden ratio of 0.618 in motion detection, or possibly in the visual signal abstractions.

4-3-11. Sigmoidalshaped response-displacement curves.

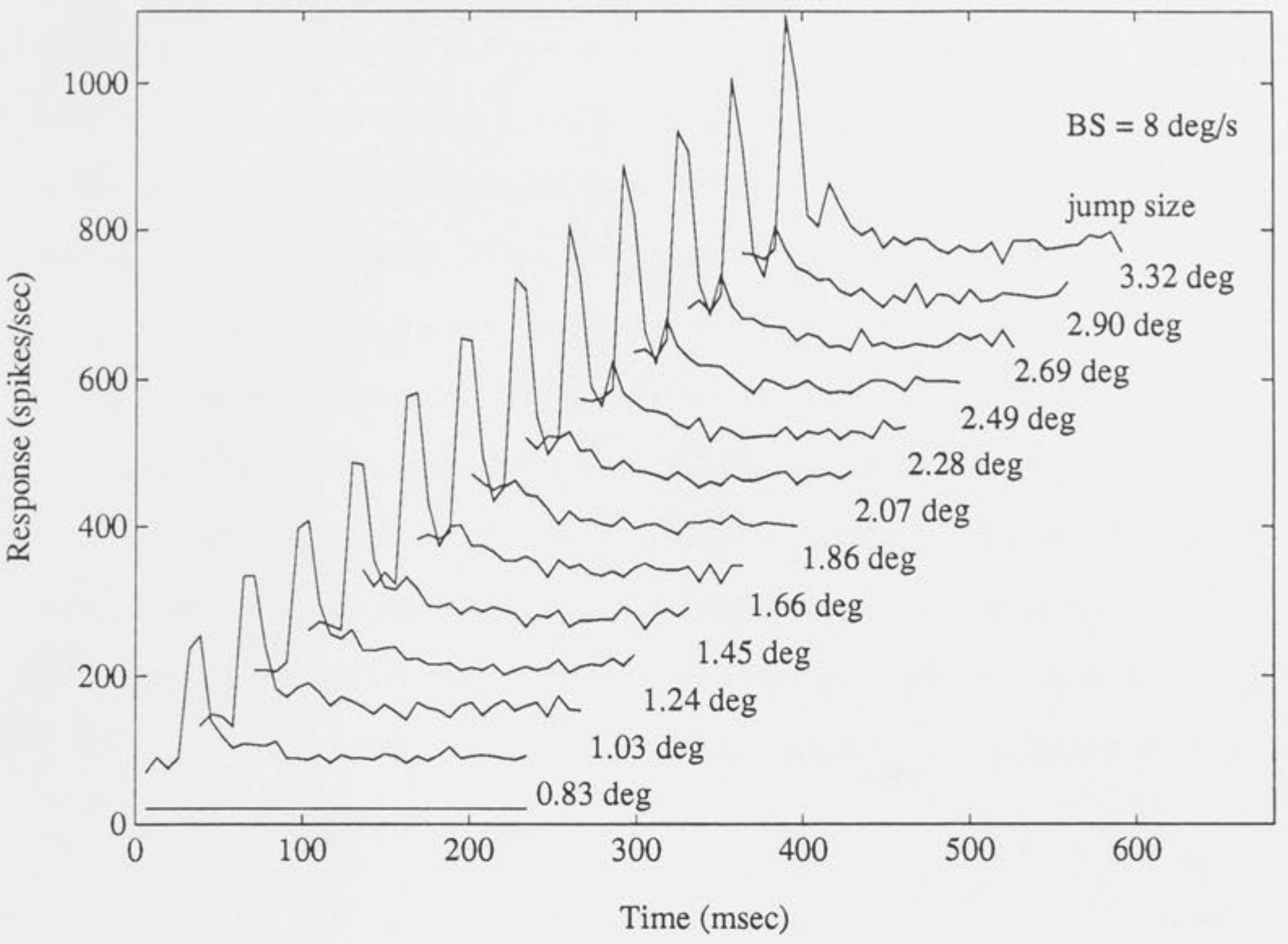
Another influence of prior-motion is to change the course of the response. The experiments were done on two H1 neurons (cell 100 and cell 102) and two V2 neurons (cell 101 & cell 103). The responses, measured for the range of jump distances from 0.2° to 3.4° for a bar that prior-moved at two different speeds, i.e, 8 °/s (for cell 100 & cell 101) and 16 °/s (for cell 102 & cell 103), are shown in

figure 4-15 (cell 100 and cell 102) and figure 4-16 (cell 101 & cell 103). Comparing the responses of the other H1 neurons (for example, cell 85 Fig.4-11), these two H1 cells exhibit a slight difference, in that the negative phase of the responses of the H1 neurons was not so significant as observed before. However, the responses of the V2 neurons still possess a strong negative phase, behaving in the way that we described before. This may be a indication that the influence of prior-motion is less on the response of H1 than on V2, giving a hint that motion detection in the vertical-direction involves more lateral inhibition than in the horizontal direction.

The response-displacement curves of the responses of these cells, under the influence of prior-motion, are plotted in figure 4-17a (for the H1 cells) & 4-17b (for the V2 cells). All exhibit a significant difference from the curves without prior-motion, whether the response drops down or not as the bar jump angle increases. The responses of those cells which are responding to a stimulus with prior-motion simply increase their firing frequency and eventually saturate. The V2 neurons (cell 101 & 103) increase their firing frequency sigmoidally as the bar jumps from 0.2° up to 1.5°, and then saturate; but, the responses with 16 °/s prior-motion were considerably weaker than with 8 °/s prior-motion. The two response curves appear to be parallel when plotted against the bar jump angle, showing the same dependence on the speed of the prior-motion. The responses of H1 neurons (cell 100, 102) are different in that they never saturate. The bar jump angle reached 3.4° which, is equal to the width of the bar, so that it was the biggest jump size ever used in the experiments, and it achieved a firing frequency of 400 spikes/s. In contrast, the responses that are generated by the stimulus without prior-motion, always drop down when the bar jump angle is larger than about 1.2°, as already demonstrated repeatedly.

Figure 4-15. The responses of H1 to a brief jump of a black bar of width 3.32° with prior-motion. (a) Cell 100 responded to the bar jump distances from 0.83° to 3.32° with the background speed 8 °/s (a). (b) Cell 102 responded at the background speed 16 °/s with jump distances from 0.2° to 2.69° (b). The following points can be seen in the responses in (a) and (b), it is found that. First, the neuron can pick up a very small and short difference in velocity changes, demonstrated by the considerable response to the bar jump of only 0.2° (in 6.5 ms) when the background speed was 16 °/s. This value is very close to the threshold of 0.15° in the case of a jump (6.5 ms) without prior-motion, and is a clear indication that the neuron is as sensitivite to a small and short movement in the flying state as in the stationary state. Second, the neuron exhibits a significant difference in the responses to the bar jump with and without prior-motion. The neuron retained a higher firing frequency in response to a larger angular distance jump with prior-motion; in contrast, without prior-motion, the response was always reduced when the bar jump angle was larger than 1.5° (Fig. 4-8).

(a) Response of H1 to a bar brief jump (6.5 ms)



(b) Response of H1 to a bar brief jump (6.5 ms)

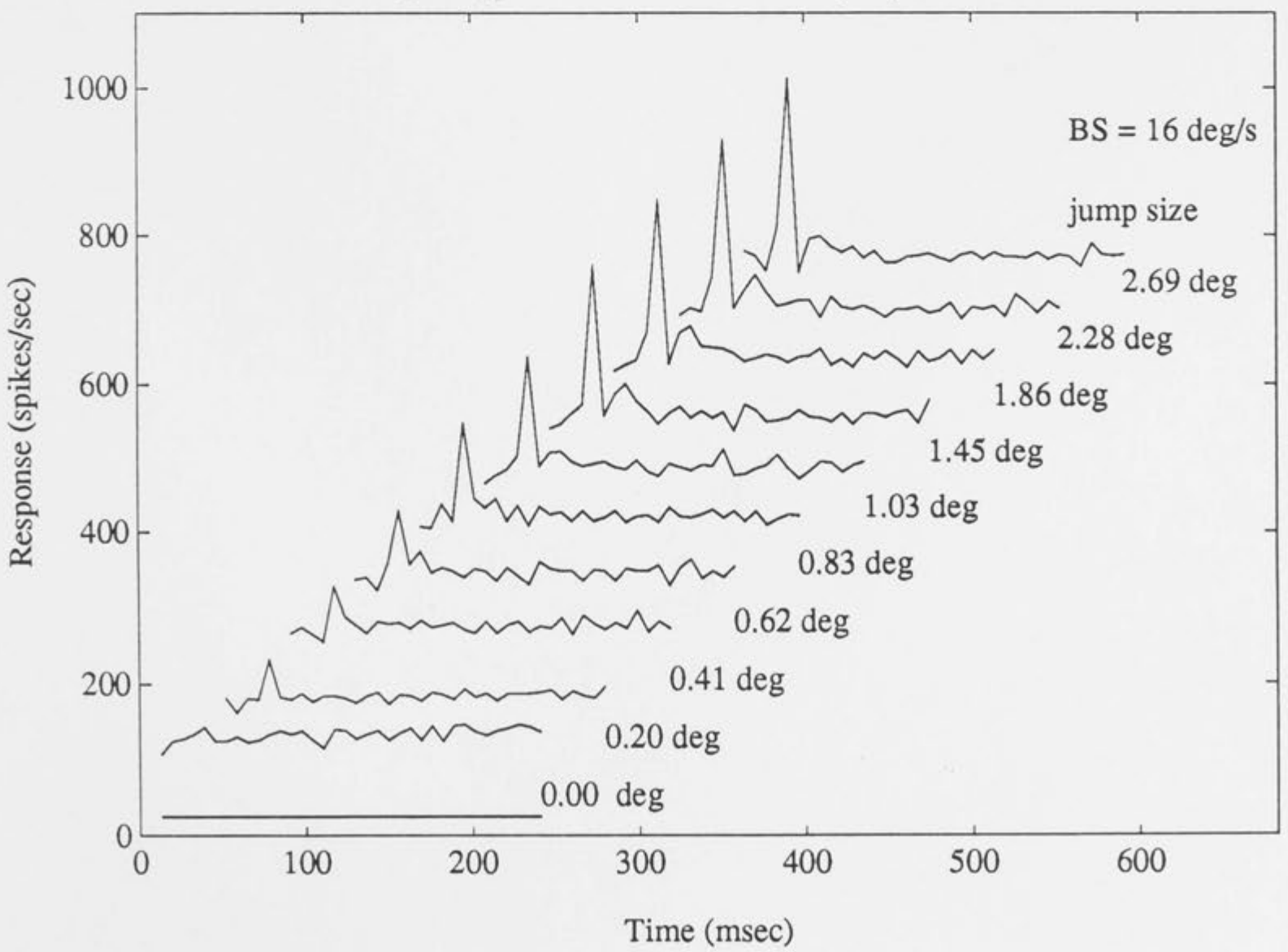
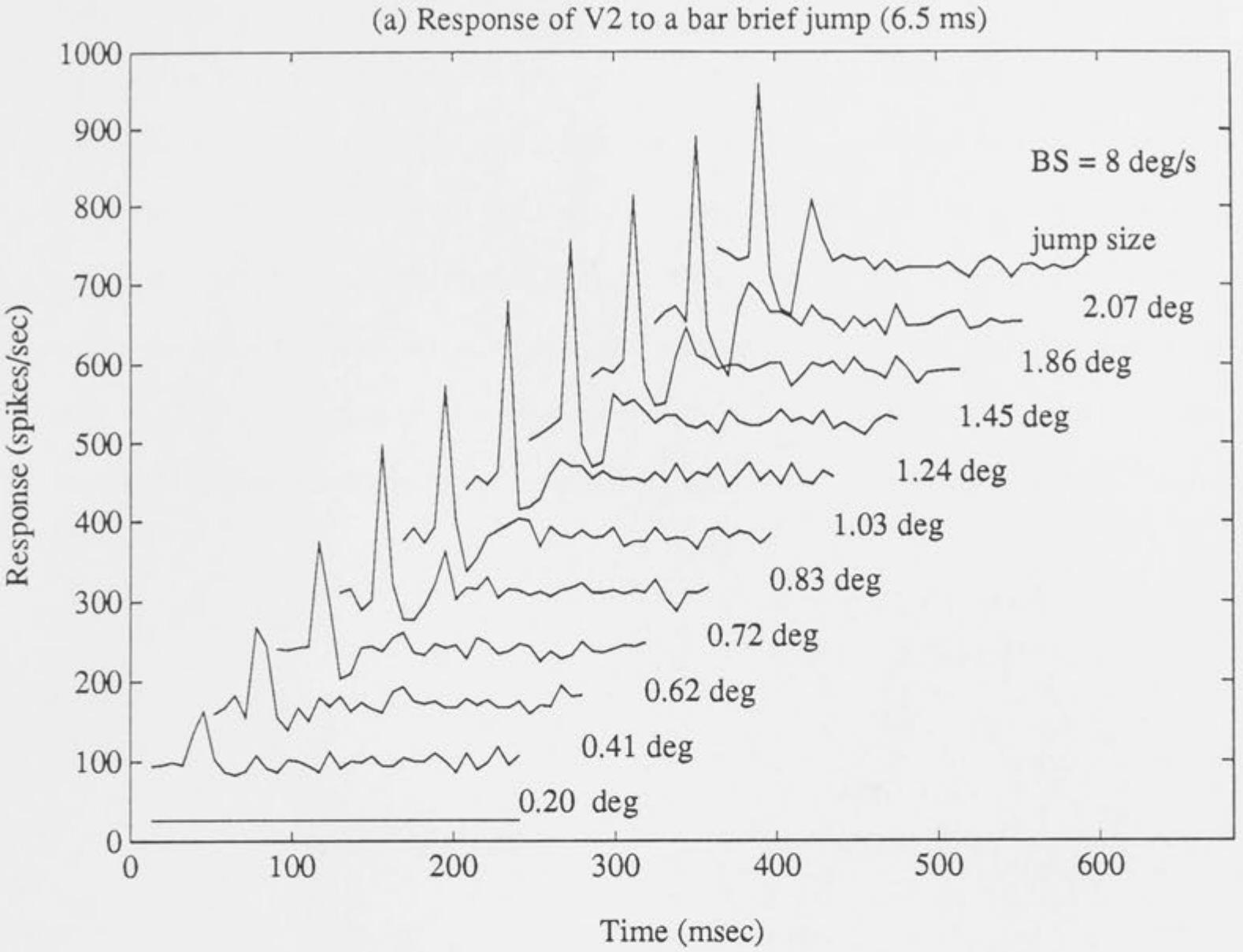


Figure 4-16. The responses of V2 to a brief jump of a black bar of width 3.3° with the prior-motion. Two V2 neurons (cell 101 & cell 103) were recorded with the bar jumping various distances between 0.2° and 3.11°, also the background speeds were set at 8 °/s (a) and 16 °/s (b). As the bar jump distance increased, the cells increased their firing frequency like the H1 neuron (Fig. 4-15), irrespective of background speed. Also, the cells produced a clear transient response to the bar jump 0.2°, indicating that the H1 and V2 neurons have a similar sensitivity to this stimulus. However, a significant difference appears when compared to the H1 response, in that V2 has a strong negative phase when the jump distance is larger than 0.62° for 8 °/s of prior-motion, or larger than 0.41° at the background speed of 16 °/s. The negative phase presumably is due to lateral inhibitory effects between the EMDs, so that V2 has more stronger lateral inhibitory effects than H1.


(a) Response of V2 to a bar brief jump (6.5 ms)
Response (spikes/sec)
Time (msec)
BS = 8 deg/s
jump size
2.07 deg
1.86 deg
1.45 deg
1.24 deg
1.03 deg
0.83 deg
0.72 deg
0.62 deg
0.41 deg
0.20 deg
0
100
200
300
400
500
600
700
800
900
1000

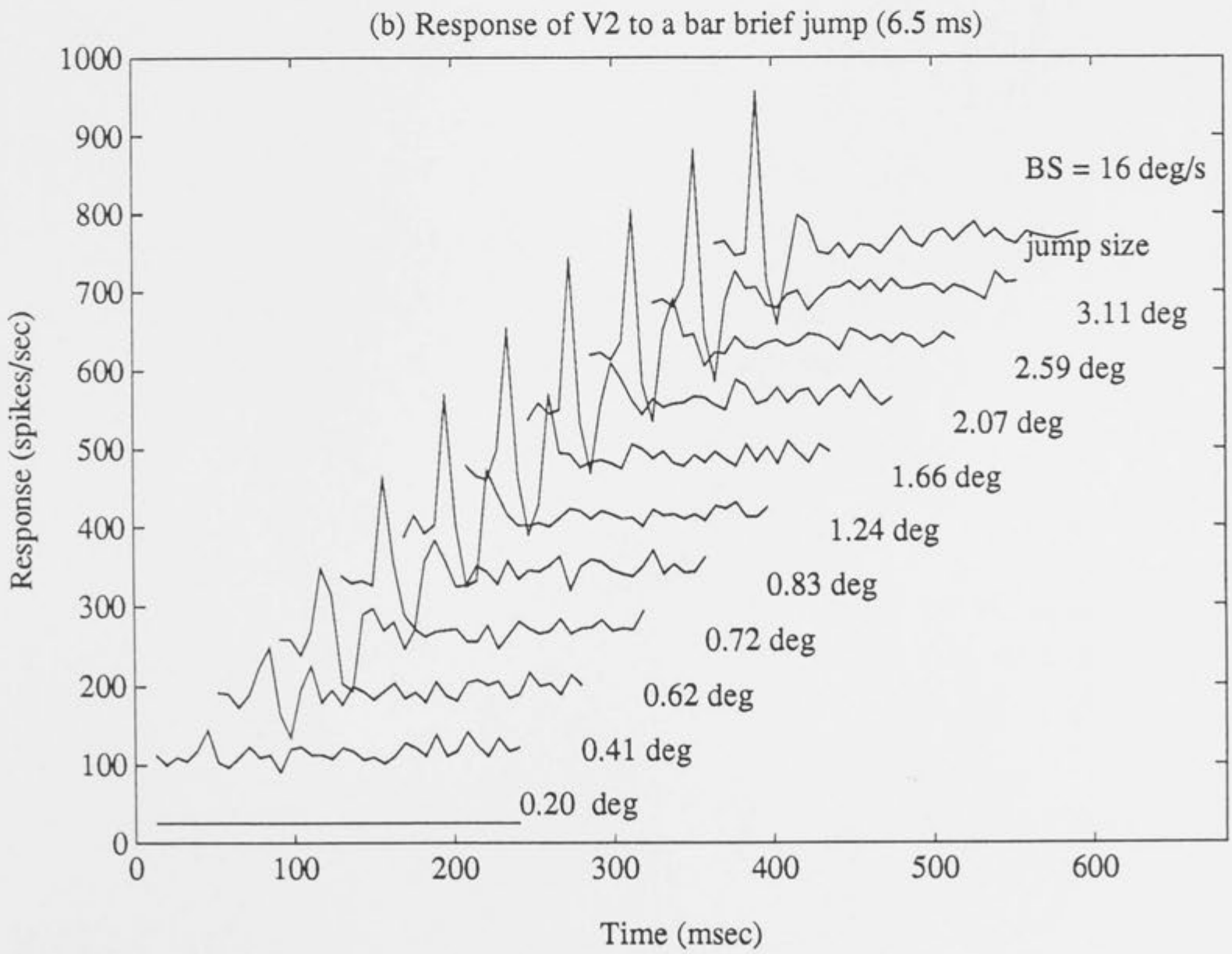
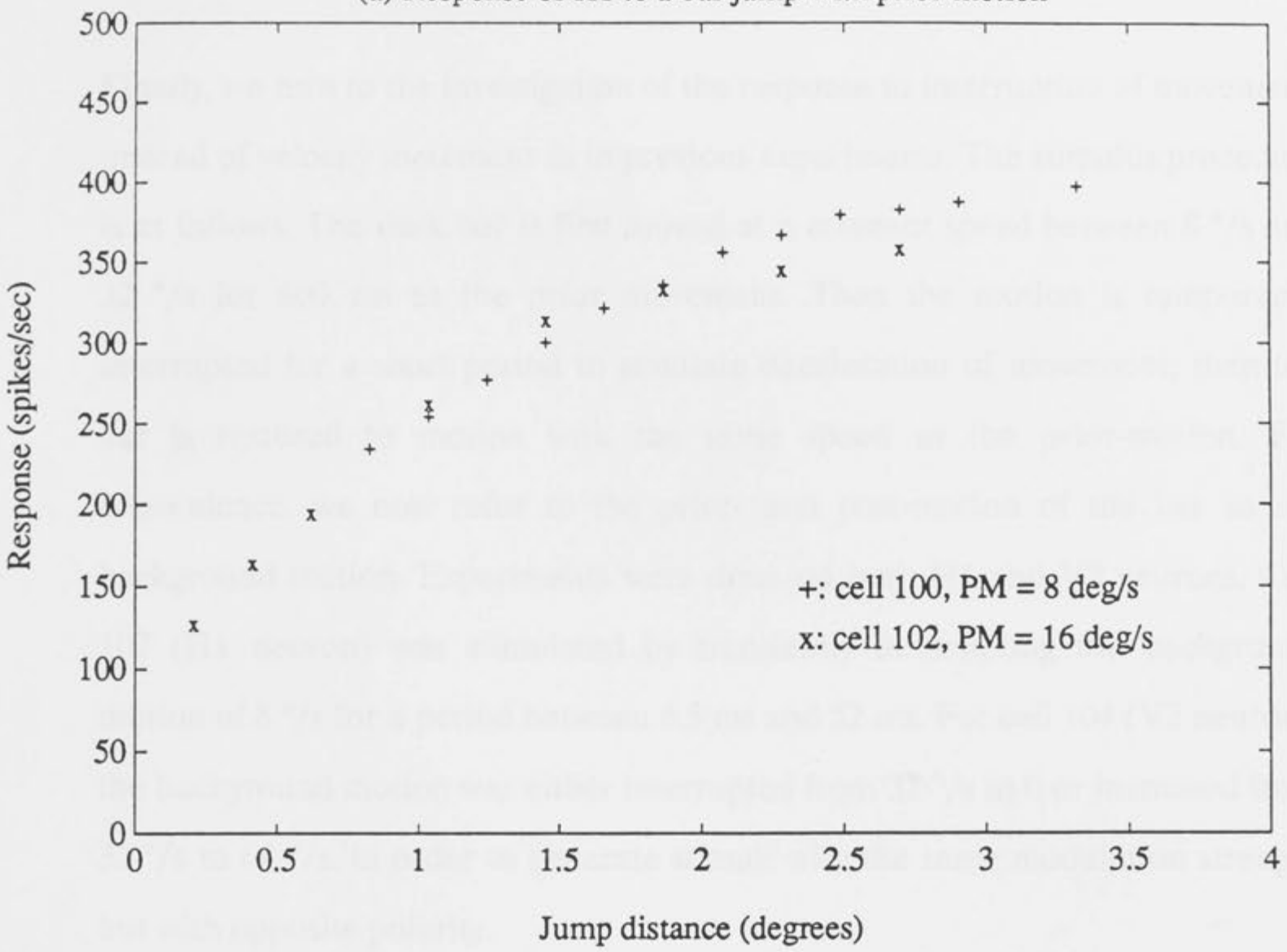
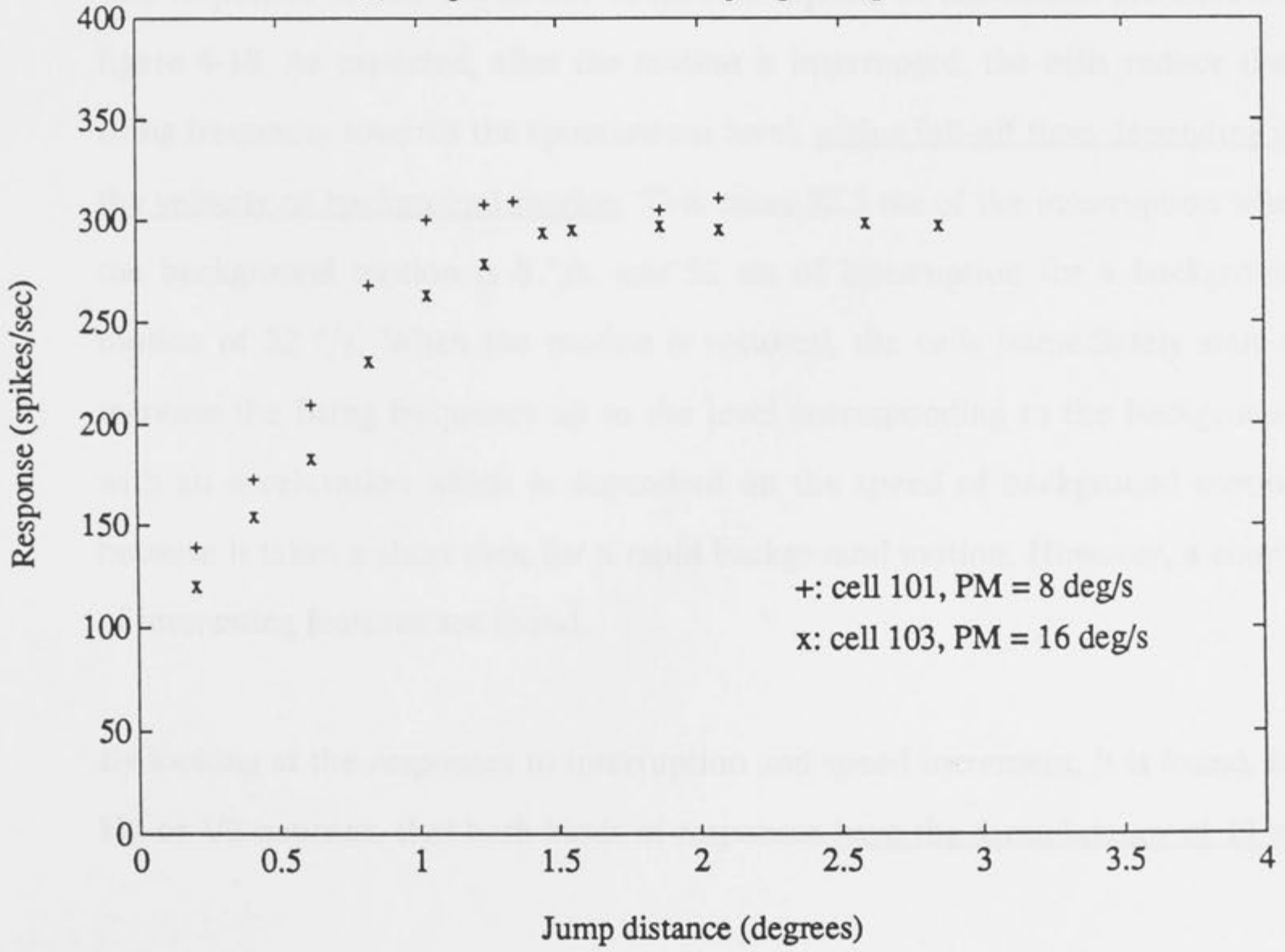

(b) Response of V2 to a bar brief jump (6.5 ms)
Response (spikes/sec)
Time (msec)
BS = 16 deg/s
jump size
3.11 deg
2.59 deg
2.07 deg
1.66 deg
1.24 deg
0.83 deg
0.72 deg
0.62 deg
0.41 deg
0.20 deg
0
100
200
300
400
500
600
700
800
900
1000

Figure 4-17. The H1 and V2 neurons possess a sigmoidal-shaped response-displacement curve when influenced by prior-motion. Comparing these with the response-displacement curves in Fig. 4-9a, where the stimulus was also a black bar of width 3.3° but without prior-motion, we now find sigmoidal-shaped or monotonic response-displacement curves. As the bar jump distance increased, the responses first increased and then saturated. In contrast, without prior-motion, the responses of H1 and V2 would drop down when the bar jump angle was larger than about 1.5° (Fig. 4-9a). This difference must reflect some unknown characteristics of motion detection.

(a) Response of H1 to a bar jump with prior-motion



(b) Response of V2 to a bar jump with prior-motion



4-3-12. The response to interruption of movement.

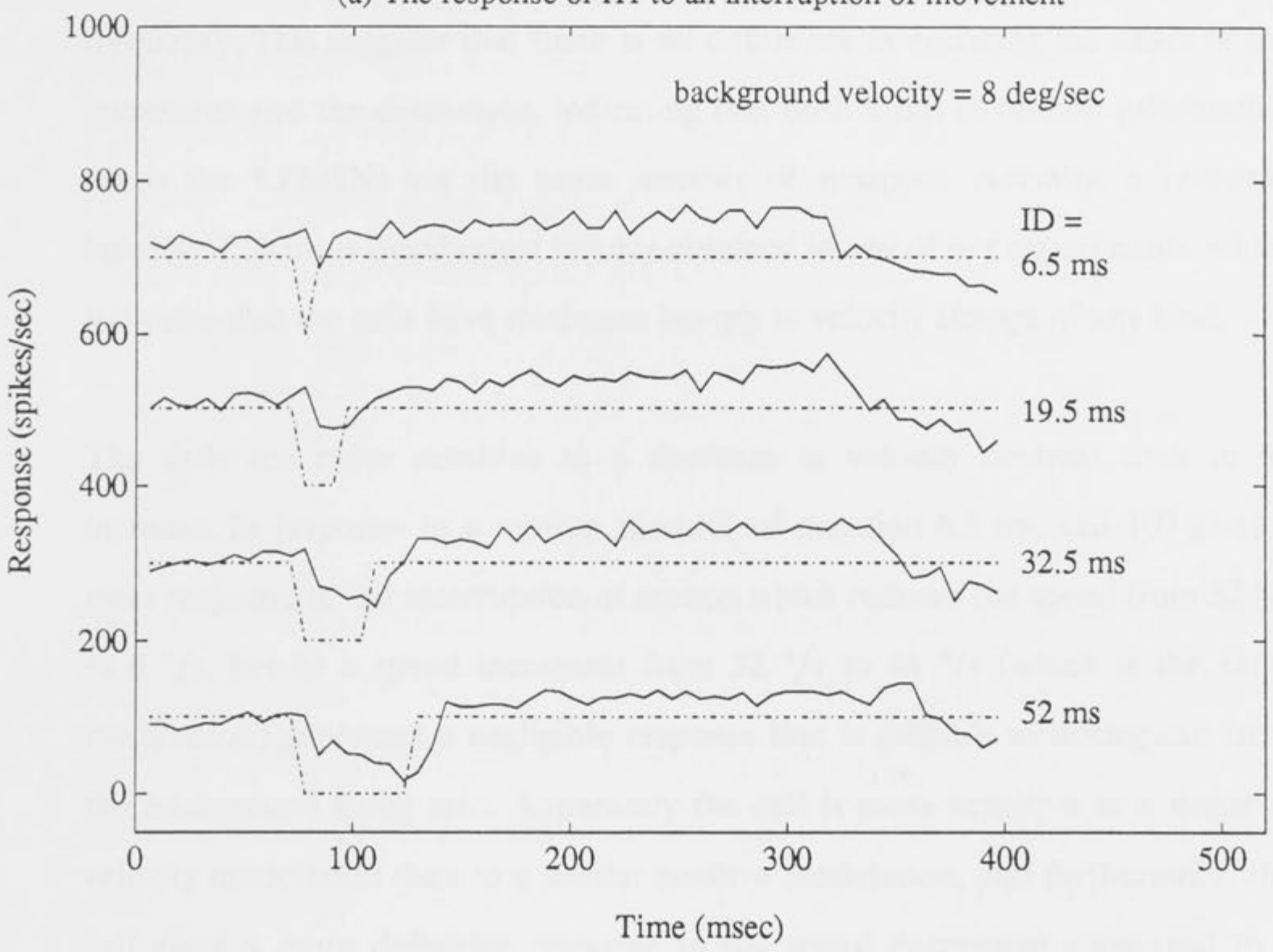
Finally, we turn to the investigation of the response to interruption of movement, instead of velocity increment as in previous experiments. The stimulus procedure is as follows. The dark bar is first moved at a constant speed between 8 °/s and 32 °/s for 800 ms as the prior movement. Then the motion is temporarily interrupted for a short period to simulate deceleration of movement; then the bar is restored to motion with the same speed as the prior-motion. For convenience, we now refer to the prior- and post-motion of the bar as the background motion. Experiments were done on both H1 and V2 neurons. Cell 107 (H1 neuron) was stimulated by transiently interrupting the background motion of 8 °/s for a period between 6.5 ms and 52 ms. For cell 104 (V2 neuron), the background motion was either interrupted from 32 °/s to 0 or increased from 32 °/s to 64 °/s, in order to generate stimuli with the same modulation strength but with opposite polarity.

The responses of cell 104 & 107 to an interruption of movement are shown in figure 4-18. As expected, after the motion is interrupted, the cells reduce their firing frequency towards the spontaneous level, with a fall-off time depending on the velocity of background motion. This takes 32.5 ms of the interruption when the background motion is 8 °/s, and 52 ms of interruption for a background motion of 32 °/s. When the motion is restored, the cells immediately start to increase the firing frequency up to the level corresponding to the background, with an acceleration which is dependent on the speed of background motion, because it takes a short time for a rapid background motion. However, a couple of interesting features are found.

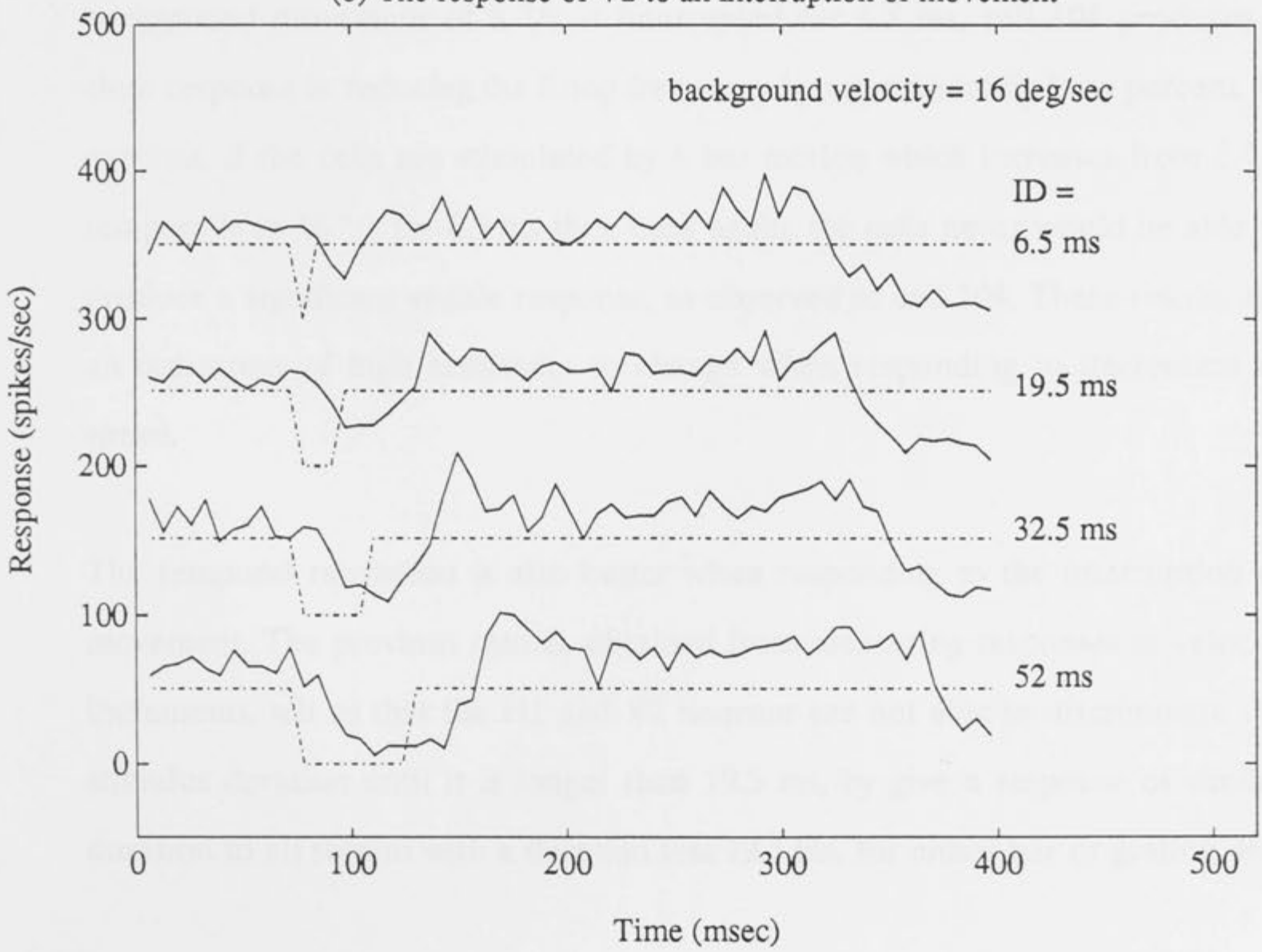
By looking at the responses to interruption and speed increment, it is found, for H1 or V2 neurons, that both kinds of responses have the same latency of 13 ms

Figure 4-18. The responses of H1 and V2 to an interruption of movement. The stimulus pattern was a black bar of width 3.3°, which moved at constant speed through the screen, but was temporarily interrupted at the centre of the screen for selected periods between 6.5 ms and 52 ms. The experiments were done on both H1 (cell 107) and V2 (cell 104). The dashdot lines indicate the duration of the interruption, and the solid lines present the responses. When the motion was interrupted, as expected, the both cells immediately reduced their spike firing frequency gradually towards the spontaneous firing level for up to 52 ms, which represents some kind of decay time. Both H1 and V2 can faithfully interpret the duration of interruption, in that the width of the response interruption is almost as same as the duration of the interruption over the whole range. This is in contrast to an incement of speed, in which the neurons always generated the responses with the same width to any movement whose duration falls in the integration time (Fig. 4-5). Finally, the cells are very sensitive to interruption of the movement, giving a "response" to an interruption of only 6.5 ms in the background speed 8 °/s. In contrast, the same neurons hardly produce a significant response to a speed of 8°/s for 6.5 ms. Also, the "response" latency was only 6.5 ms, which is shorter than the response latency to movement (Fig. 4-9d).

(a) The response of H1 to an interruption of movement



(b) The response of V2 to an interruption of movement



to change in velocity, measured to the beginning of the change in firing frequency. This suggests that there is no difference in encoding the onset of the increment and the decrement, indicating that both kinds of motion information reach the LFMSNs via the same number of synapses. Actually, a response latency of 13 ms is the shortest latency obtained in any of our experiments, which indicates that the cells have minimum latency to velocity change of any kind.

The cells are more sensitive to a decrease in velocity contrast than to an increase. In response to a motion stimulus of duration 6.5 ms, cell 107 gives a clear response to the interruption of motion which reduces the speed from 32 °/s to 0 °/s, but to a speed increment from 32 °/s to 64 °/s (which is the same modulation) generates a negligible response that is difficult to distinguish from the background firing rate. Apparently the cell is more sensitive to a negative velocity modulation than to a similar positive modulation, and furthermore, the cell gives a more definitive response to the speed decrement compared to a speed increment. The same result is obtained from the V2 neuron; when a background movement of 8 °/s is interrupted for 6.5 ms, cell 104 produces a clear response in reducing the firing frequency by approximately forty percent. In contrast, if the cells are stimulated by a bar motion which increases from 8 °/s temporally to 16 °/s for 6.5 ms then back again, the cells never would be able to produce a significant visible response, as observed in cell 104. These results are an indication of high sensitivity to change when responding to decrement of speed.

The temporal resolution is also better when responding to the interruption of movement. The previous results, obtained from measuring responses to velocity increments, tell us that the H1 and V2 neurons are not able to discriminate the stimulus duration until it is longer than 19.5 ms, by give a response of similar duration to all stimuli with a duration less 19.5 ms, for either bar or grating. But

with decrements, the cells are able to tell the difference in the temporal length of the interruption, even the difference between 6.5 ms and 13 ms interruptions. For example, the response duration of cell 107, measured from the start of the response decrement to the beginning of the response restoration, is exactly equal to the duration of the interruption, exhibiting the capability of distinguishing the temporal length of the interruption accurately. In contrast, when responding to velocity increment, the same cells are poor in discriminating these temporal differences.

The integration time of lateral inhibition of the cells keeps constant, however, when responding to the interruption. This is proved by a simple fact that the response to motion restoration is a transient peak when the interruption period was longer than 19.5 ms. This means that after an interruption of 19.5 ms or longer, the lateral inhibition from preceding units has lost its influence on the response of the later units, resulting in the appearance of a transient peak when motion is restored. This period of time is similar in the duration of the lateral inhibition, which is about 19.5 ms in the above experiments. So we can say the lateral inhibition keeps constant temporal relations when the cells are responding to the interruption of movement. Actually, these results agree with the idea that the integration time of lateral inhibition is determined by the connections of the EMD's, and not by the form of the stimulus.

4-4. Discussion and conclusion

From the analysis of the response to brief bar jumps with/without prior-motions in the experiments of 4-3s, we are able to reach several conclusions about the spatial structure of the motion detectors.

4-4-1. Non-linear spatial integration.

The response of the large field motion detectors to movement of any stimulus must be due to non-linear spatial integration of many elementary unit responses. Tests of local spatiotemporal resolution of all kinds prove this beyond doubt. The response amplitude to a single bar is similar to that to an extended grating of eight bars (see 4-3-1), suggesting that there is a strong non-linear lateral interaction between the EMD's during spatial integration. Without lateral interaction, the response strength to the moving bar should be much less than that to the moving grating. Although we do not dismiss the affect of response saturation, this phenomenon looks like a strong lateral inhibition between the EMDs. The evidence of lateral inhibition also comes from other findings. Firstly, a negative response phase is observed when the speed of bar motion suddenly changed, as if the EMDs respond to the prior-motion of bar by a strong inhibition to the EMDs responding later, so causing a negative phase. Secondly, the transient response strength decreases as the bar displacement angle increases after the angle is greater than a certain limit, indicating that there is a lateral inhibition field or a lateral inhibition threshold in terms of stimulus strength.

The existence of lateral interaction in the neural network is also supported by the findings in 4-3-6, in which the response decreases as the bar jump angle increases, after the jump distance is bigger than a certain angle. One of

explanations about this phenomenon is that probably there is a local lateral inhibition between the EMDs which is active in a relatively short time period at the level that the responses of the EMD's are combined, causing the response of H1 and V2 to eventually drop down when the bar jump angle is so large that the interneurons actually can be inhibited by the neighbouring units during this short integration period, or may be outside the field of the EMD. The idea is supported by comparing the two kinds of the response-displacement curves, Fig.4-9a and Fig.4-3. The response (Fig.4-3) to a moving grating never drops as much as those to a jumping single bar (Fig.4-9a). Instead, the response to a grating either saturates at a high level or falls only slightly, which reflects that, to a stimulus of grating, all EMDs are at the same state, so that the response of the LFMDs only saturates and never declines as the grating jump angle increases. In fact, the lateral inhibition has a limited range in both spatial and temporal domains. Its interaction in time might be as short as 6.5 ms, or within one synapse transformation time; and its influence may be limited only to the neighbouring EMD's.

4-4-2. Probable structure of the EMDs.

The transient part of the motion detector neuron response appears to be a reflection of the characteristics of the individual EMD units, as supported by our previous results and proposed by others (Egelhaaf et al 1989). The measure of response acceleration in the transient phase against the stimulus displacement might provide a practical way in which to evaluate the size of the unmodified receptive field for a single EMD. Supposing, if the LFMD consists of a large number of spatially symmetrical EMDs, the minimum distance moved by a jump to give a just saturated response could be considered as the distance between EMDs. Because beyond this point the contiguous EMDs will be consecutively stimulated, causing the response to remain at a constant saturated level. On this

assumption we predict that the distance between two adjacent EMDs is about 1.7° in both horizontal and vertical directions. Interestingly we found that the EMDs of both H1 and V2 had the same temporal and spatial characteristics, for example, about 0.6 degree linear integration distance, and 32 ms transient period, in response to a motion stimulus of 16 °/s (see the experiment of 4-3-1).

Of course, the size of an EMD's receptive field depends on how it is defined. The curve of the transient response versus stimulus displacement has a triangular or bell-shaped profile with 2.5°±0.3° width at the 50% level (in the experiments of 4-3-6 and 4-3-7). This phenomenon must reflect the characteristics of the EMDs, which probably possess a triangular or bell-shaped receptive field with an effective width of 2.5°±0.3° at 50% level, in agreement with many previous findings (Arnett 1971a & b; Buchner 1976). This spatial parameter may be related to the interommatidial angle, but of course is not necessarily equal to it, as was suggested by Zaagman et al. (1978); also, that we used a bar not a light point in the measurement.

The wide-field motion sensitive neurons of the lobula plate, such H1 and V2, then collect the outputs of these EMDs to give a response to the next stage, and they have similar spatial parameters, suggesting that they collect responses from EMDs with similar physiological properties.

4-4-3. The dependence of the neurons response on stimulus displacement.

As shown in the response-duration curves in 4-3-2, the transient response of the cells is dependent on the stimulus displacement during the integration time, in a full agreement with previous findings (Srinivasan 1983). In other words the motion of the bar is integrated by the cells over an initial transient period, irrespective of how the stimulus speed and duration of motion is distributed in

the temporal domain. The motion of the stimulus is also linearly integrated by the cells over the first 0.43 degrees of displacement, but the H1 and V2 neurons appear to be unable to measure the velocity and displacement independently, since the integration time is dependent on the stimulus velocity (seen in 4-3-2).

In the experiment with a bar jump (4-3-7), the strength of the transient response of H1 and V2 depends linearly upon the jump angle at both sides of a critical optimum angle of about 1.1° degrees. During the initial linear response range, the average slope of the plot of transient response against the bar jump angle is about 250 spikes per second per degree displacement. This slope, which I term the angular distance discrimination coefficient, is a convenient measure of the neuron's ability to measure the spatial displacement of a bar. Also, the experiment of 4-3-6 shows that the H1 and V2 neurons are similar in response to displacement, except that the horizontal component of the EMD's response is bigger than its vertical component.

The H1 neuron normally has a higher background and response firing frequency than the V2 neuron perhaps because at each location within the receptive field, the response of the H1 cell to horizontal motion is produced by summation of two neighbouring elementary motion detectors, with preferred direction that are 30° degree above and below the horizontal axis of the eye. The inputs of V cell on the other hand, consist of only one set of vertically oriented EMD's (Buchner E 1976, Hateren JH van 1990) so that the response of the H cells should be always larger that the response of the V cells. The difference provides a higher gain for visual stabilization in the horizontal than in the vertical phase.

4-4-4. The velocity measurement of the large field motion detectors.

From analysing some fundamental parameters of the response, such as the peak firing frequency, the plateau level, the initial slope of the response, the latency and the time to peak, versus the speed of a moving bar (in experiments of 4-3-4), it is suggested that the H1 and V2 neurons can measure velocity in terms of these parameters by their response in both transient and steady state, but they act only in a relatively narrow range of motion. They are capable of encoding the velocity nearly linearly over a range of 0 to 58.8 deg/s in the transient response, and up to 42 deg/s in the steady state. There are no differences between the H1 and V2 neurons in these quantitative measures.

This maximum discriminable velocity (58 deg/s) is not particularly high in comparison with the velocities that occur naturally in flight. If we assume that the EMDs are composed of two neighbouring simple photoreceptors with integration time of 10ms (the shortest period obtained in experiments) and receptive field about two degrees wide, the EMDs should be able to register motion speeds up to approximately 200 deg/s. The assumption could be supported by a roughly calculation about the EMDs velocity discrimination in another way; if the neuron can discriminate a brief bar jump up to 1.1° in 6.5 ms (see 4-3-7), it should be able to distinguish the bar velocity over a range up to 170 deg/s. This transient property, of course, represents the EMDs. However, the measurement of velocity is obviously distorted because there is the same strength of response to two different speeds on either side of the critical speed of 170 deg/s.

This phenomenon therefore suggests that H1 and V2 may abstract features of motion other than just the speed, a point which will be discussed in a following chapter. Also, the question still remains whether these particular properties that

are measurable from the phasic response are those to which higher-order neurons might be sensitive in subsequent processing of the signal.

4-4-5. Temporal resolution versus integration time.

It is obvious that the temporal resolution of the motion detection neurons is related to the integration time. In the other words, the integrating time has a direct effect on the temporal resolution of the cells with respect to motion detection.

The experiment of 4-3-3 demonstrates that at the onset of motion the stimulus motion is integrated in the time domain, and that the period of the integration time is strongly dependent on the velocity of the stimulus, so that fast motion only needs a short duration and slow motion needs a long duration. So, the temporal resolution of the bar motion improves with increasing bar speed. In our experiments the shortest integration time found so far is about 13 ms for the H1 and V2 neurons, thus the cells may be capable to measure a motion of about 13 ms, which is not much poorer than the temporal resolution of the photoreceptor cells with regard to registering fluctuations of intensity. Thus, the LFMDs have input time constants matched to utilize the information that the photoreceptors can measure in the temporal domain. This sensitivity is also dramatically enhanced in a faster moving environment. Interestingly, the temporal resolution in responding to interruption of movement is better than to increase, as demonstrated in the experiment of 4-3-12 that the neuron can measure 6.5 ms interruption period.

Also, the fact that cell 79 (V2 neuron) had a shorter decay time and a more prominent second peak compared to cell 69 (H1 neuron), indicates that the vertical motion detecting system possesses a better temporal resolution than the

horizontal one. This is consistent with the idea that vertical flying must be more accurate than flying in the horizontal direction, because a very slight error in the vertical direction is more significant in cases such as landing and escaping compared to the horizontal direction.

The finding that the firing frequency of the neurons included a negative phase when the jump size exceeded a critical value (see 4-3-5), suggests an additional interaction at greater angles or the presence of a feed-back loop in the motion detection system. A feed-back loop, if present, might be able to improve the temporal resolution of H1 and V2 since it could shorten the response decay time for small jumps.

4-4-6. Different kinds of channel in motion detection.

In the experiment of 4-3-11, a sigmoidal-shaped response-displacement curve is observed when the neuron responds to bar jumps with prior-motion. In contrast, the neuron gives a bell-shaped response curve to the stimulus without prior-motion (see 4-3-3). The difference may be the "memory" when there is no prior motion. This feature must be related to the structure of motion detection, and raises the possibility that there are two kinds of elementary motion detection channels or mechanisms feeding motion signals into the large field motion detector.

One kind, with bell-shaped response curves, is effective when the background is in a relatively stationary state, to detect a sudden movement from the background, with a big response to such movement, in order to tell the animal unmistakably that a target is beginning to move but they give the same strength response to two different speeds. Another kind of channel is active in the motion state, to continue the response to steady motion of a target. Therefore compared

to the first kind, the second are more sensitive, faster, and respond better to a change in velocity. This idea is in agreement with the recent findings by Osorio (1987) that the medulla of locust contains many parallel small-field motion detectors, called transient cells, with different time parameters. These cells may be components of different elementary motion detection channels, a question which will be discussed in more detail in the chapter of general discussion.

The other possibility regarding the appearance of two kinds of response curves is that there is a lateral influence between EMD's which increase the angle over which they act according to the state of the neighbouring response. If adjacent EMDs are excited, this influence shifts the peak to longer and longer jumps.

CHAPTER FIVE

THE SENSITIVITY OF THE H1 NEURON TO VELOCITY MODULATION

Abstract

The H1 neuron of the fly Lucilia cuprina is one of the wide-field motion-perception interneurons of the lobula plate. The transient response, measured as the mean spike rate over many repetitions of the same stimulus sequence, is initially large at the onset of a movement, quickly failing to a plateau and then continuing to adapt slowly when the stimulus is a steady motion of a pattern. Modulation of the velocity of the moving pattern (velocity contrast) cause a modulation of the mean spike rate, which adapts more slowly than the adaptation to the mean velocity. The modulation of the spike rate and the average maximum spike rate are both measures of the velocity modulation irrespective of the contrast frequency, mean velocity, or velocity modulation frequency up to 12 Hz. The responses are in phase with the sine-wave modulated stimulus velocity; suggesting that H1 measures dV/V_m not dV/dt, where V is the velocity and V_m is the mean velocity. If the responses of the H1 neuron are indicators of their properties, the unit motion detectors are specialized for high resolution, high gain, short latency, transient detection of direction of velocity change. These features are those required in controlling errors in stability while flight is already in progress, and other aspects of insect vision presumably are carried in other neurons.

5-1. Introduction

5-1-1. Motion detection by the H1 neuron.

Notwithstanding the obvious phasic properties of the H1 neuron, most investigation have been concerned with the steady state response to continuous motion, or to various mimics of continuous motion with two modulated light sources or narrow bars with 90° phase difference. The H1 neuron detects small movements of localized contrasts towards the preferred direction anywhere in its large visual field. The optimum local displacement of a small target is about the same as the angle between visual axes, and the H1 neuron acts like a funnel which collects excitation from many unit directional motion detectors at the highest resolution available to the retina. The H1 neuron has been accepted as a representative of the numerous lobula plate neurons which reveal the properties of the elementary motion detectors of the fly (Hausen & Egelhaaf 1989, Franceschini et al 1989). The actual function of the H1 neuron in the processing circuitry is in doubt because it responds to horizontal motion towards the anterior, and its axon connects the two optic lobes.

5-1-2. Adaptation of the H1 neuron.

Adaptation takes two forms. First, the H1 neuron responds strongly to the onset of a forward horizontal movement across the eye, and the response quickly falls to a plateau then continues to fall more slowly while the motion is maintained at constant velocity. Over the short term, the fall in the response is approximately exponential, $R = r(1 + k^{*}\exp(-at))$ where r is a low background spike rate, k is a response constant depending on stimulus strength, and a is a time constant. This form of adaptation suggests that the H1 neuron does not have a function related to steady state motion. The second form of adaptation is a shortening of the time

constant a when the frequency of passing contrasts is increased. This form of adaptation has the effect that the temporal resolution for the detection of changes in the motion of the stimulus is improved by the motion itself. This increase in temporal resolution is controlled locally by the stimulus and does not depend on the impulse ferquency of the H1 neuron. When we put together both types of adaptation, we see that local motion detectors adapt in response to local motion in much the same way that photoreceptors do to their own signal, light intensity (Maddess & Laughlin 1985). Light adaptation of photoreceptors and of the second-orger neurons, the lamina ganglion cells, is also accompanied by an improvement in temporal resolution (Laughlin 1981). As a consequence of adapting to background intensity, photoreceptors provide a measure of dI/Im where I is the light intensity and Im is the mean intensity - the well known Weber relationship.

As a test of the effects of adaptation, Maddess and Laughlin demonstrated for the H1 neuron.

(a) An increase in sensitivity to a small decrements and increments of the velocity of a moving random pattern with increase of the background adapting velocity.

(b) Responses to a fixed increment or decrement of velocity contrast are reasonably independent of the adapting velocity.

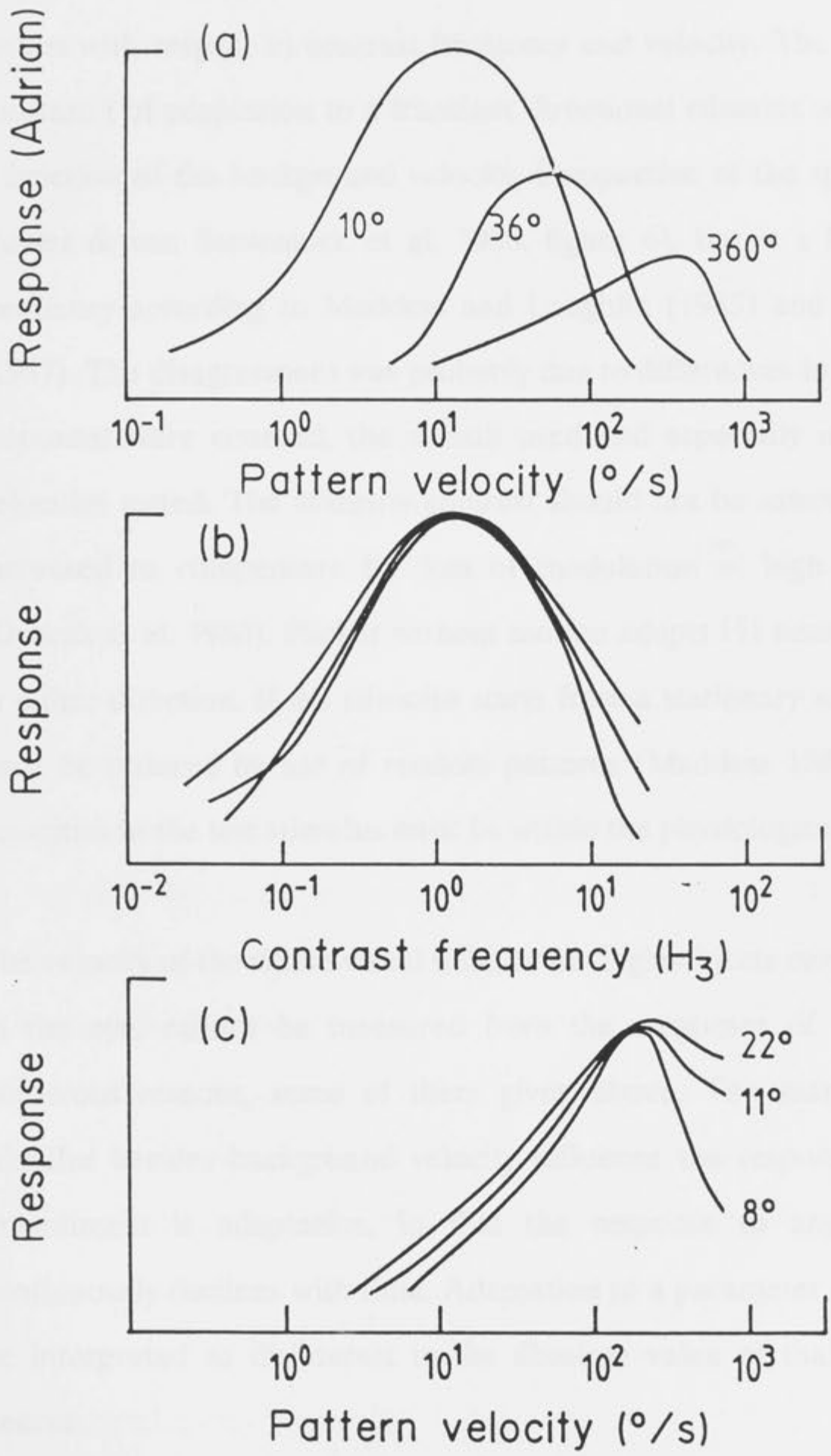
In (a) only one adapting velocity was used, and in (b) only one velocity contrast was tested at five adapting velocities over the range from 3 °/ to 100 °/s. We have confirmed this work and extended it to a range of contrast, spatial frequency, background velocity, velocity modulation, frequency, and background contrast frequency.

5-1-3. Contrast frequency, velocity and spatial frequency.

Over the past 30 years it has become accepted that the optomotor behaviour and the response of the associated neurons of the lobula plate of the fly to a moving regular striped pattern are a function of the contrast frequency irrespective of spatial frequency rather than the velocity of the stimulus irrespective of pattern (Eckert & Hamdorf 1981). This applies also to the worker bee (Kunze 1961) and to directionally sensitive neurons of the butterfly medula (Horridge & Marcelja, unpublished data: Ibboston et al 1990). These features are illustrated for the fly H1 neurons in figure 1a, b. When the average transient responses over a given period after onset of the stimulus are plotted against pattern velocity, a different bell-shaped curve is obtained for each spatial frequency (Fig 5-Ia), but when the responses are plotted against the contrast frequency generated by the same motion, the bell-shaped curves more or less coincide (Fig 5-Ib). When the stimulus is a regular stripe pattern and the responses are summed, this result is to be expected from any system which gives a unit response to each edge passing the motion detectors. We are tempted to infer that a system with this dependence on pattern can form only a part of the visual processing mechanisms because flying insects behave as if they can measure the angular velocity of contrasts irrespective of their spatial or contrast frequency.

Without explanation, other workers have found a different behaviour in some other insect directional motion-detectors. In wide-field motion detectors of the locust brain (Kien 1975, figure 3), motion detectors of the dragonfly ventral cord (Oldberg 1981, figure 8) and in the control of flight speed by Drosophila (David, C.T 1982) the curves coincide when the responses to different spatial frequencies are plotted against velocity rather than against contrast frequency (figure 5-Ic), showing that the response to velocity is independent of pattern. More recently, the template model (Sobey & Horridge 1990) provides a completely different

Figure 5-I. Stylised response from previous work to illustrate the significance of contrast frequency. (a) Response (measured as spike frequency over a set time long after the onset of the stimulus) of the fly H1 neuron, plotted against pattern velocity at three different stripe periods, 10°, 36° and 360°. (b) The same response normalised to 100% and plotted against the contrast frequency. (c) Responses of a dragonfly self-movement detector neuron plotted against pattern velocity for stripes 8°, 11° and 22° period. (a and b after Eckert 1980; c after Oldberg 1981).


(a)
Response (Adrian)
10°
36°
360°
10^{-1}
10^{0}
10^{1}
10^{2}
10^{3}
Pattern velocity (°/s)
(b)
Response
10^{-2}
10^{-1}
10^{0}
10^{1}
10^{2}
Contrast frequency (H_3)
(c)
Response
22°
11°
8°
10^{0}
10^{1}
10^{2}
10^{3}
Pattern velocity (°/s)

way of explaining all the responses of the neurons and of the whole insect visual behaviour.

Studies on the adaptation rate of the H1 neuron itself have even found opposite results with respect to contrast frequency and velocity. The control of the time constant $\underline{t}$ of adaptation to a transient directional stimulus was considered to be a function of the background velocity, irrespective of the spatial frequency (de Ruyter & van Steveninck et al. 1986, figure 6), but is a function of contrast frequency according to Maddess and Laughlin (1985) and Borst and Egelhaff (1987). The disagreement was probably due to differences in the time over which responses were counted, the stimuli used and especially in the ranges of the velocities tested. The intensity contrast should not be saturating and should be increased to compensate for loss of modulation at high spatial frequencies (Dvorak et al. 1980). Flicker without motion adapts H1 nearly as well as motion in either direction. If the stimulus starts from a stationary state, memory effects must be reduced by use of random patterns (Maddess 1986), and the angular velocities in the test stimulus must be within the physiological range.

The velocity of the whole visual field, or of single objects moving steadily relative to the eye, cannot be measured from the responses of the H1 neuron for numerous reasons, some of them given above. Too many attributes of the stimulus besides background velocity influence the response, but the greatest impediment is adaptation, in that the response to any constant stimulus continuously declines with time. Adaptation to a parameter of the stimulus must be interpreted as disinterest in the absolute value of that parameter by that neuron.

5-2. Methods

5-2-1. The animal and preparation.

Cultured female sheep blowflies of a standard wild strain of Lucilia cuprina, were kindly supplied by CSIRO, Division of Entomology, Blowfly Genetics Group, Canberra, ACT, Australia. They were kept in natural daylight in a cool place and fed on sugar solution.

Flies were waxed to a support on a ball joint without the use of carbon dioxide. The head and eye were then aligned with the screen of a cathode ray tube (type 609 with P31 phosphor) as described by Maddess and Laughlin (1985). For optimum stimulation of the H1 neuron the flies were oriented so that a point 30° lateral to the fly's midline on the equator of the eye pointed to the centre of the screen, which subtended 54° at the eye. The H1 neuron was recorded from the contralateral side, leaving untouched the side ipsilateral to the stimulus. As in previous work, recordings were discontinued if the H1 neuron showed irregular or regular bursting responses. The recording room was in darkness, with temperature controlled at 22° ± 2°. All flies were light-adapted to their position in front of the screen, and illuminated at an average brightness of 7 cd/m*m for at least 20 min before recording. Apart from the first few seconds while they rapidly became adapted to a steady rate, the responses to velocity-modulated moving patterns were all averaged over large numbers (usually 100 repetitions) of the modulation.

5-2-2. Stimulus and recording.

The patterns were generated by a computer (PDP 11/03) with a frame rate of 160 Hz and a frame of 1024 lines. The equipment was similar to that used by

Maddess (1986). Spikes were recorded by standard methods, collected by computer, and displayed as phase-locked histograms or average numbers of spikes in bins 6.5 ms wide, under the control of hybrid Assembler/Fortran/DAOS (data acquisition operating system) software.

The stimulus was a sine-wave striped pattern controlled in average intensity, contrast, spatial frequency, average velocity, velocity modulation (=velocity contrast) and in velocity modulation frequency. Most stimulus were maintained in a steady state for periods of more than an hour, and the corresponding records are of the steady-state responses, with recording initiated many minutes after the onset of the stimulus. The recording of the averaged spike frequencies were phased-locked to the modulation of the stimulus and printed as in figure 2.

5-2-3. Definitions

Bearing. The angle on the eye. This is the direction of a stimulus with reference to the eye. The long axis of the insect is the reference zero.

Contrast frequency. The temporal frequency (Hz) of the flicker induced in an ommatidium by the movement of a contrasting striped pattern over it; see equ. 1.

Contrast frequency contrast. The change in contrast frequency relative to the average contrast frequency; see equ. 2. In the present paper this contrast occurs in time, not space.

Intensity. The absolute intensity of the stimulus, measured in photons per second per facet, or per second per cm*cm at the eye.

Intensity contrast. The relative difference in intensity of the dark and light bands in the stimulus pattern.

Modulation of Intensity. The relative change in intensity at the receptors caused by the movement of a striped pattern acrosse the eye. This is not the same as the intensity contrast in the stimulus (dI/Im) because it depends on the spatial frequency and on the optical modulation transfer function of the lens of the eye. When the spatial frequency is adjusted to keep the contrast frequency constant at a new velocity, the stimulus contrast must also be adjusted to bring the modulation of intensity back to the former constant level (Dvorak et al. 1980).

Pattern period. The angle subtended at the eye by one period of a striped pattern.

Spatial frequency. The reciprocal of the pattern period, measured in cycles/degree.

Velocity. The angular velocity of a stimulus across the eye, measured in degrees per second.

Velocity contrast. The change in angular velocity of the stimulus relative to the average velocity; see equ. 2. In the present paper the change occurs in time.

Velocity modulation frequency. The temporal frequency of the velocity modulation.

5-3. RESULTS

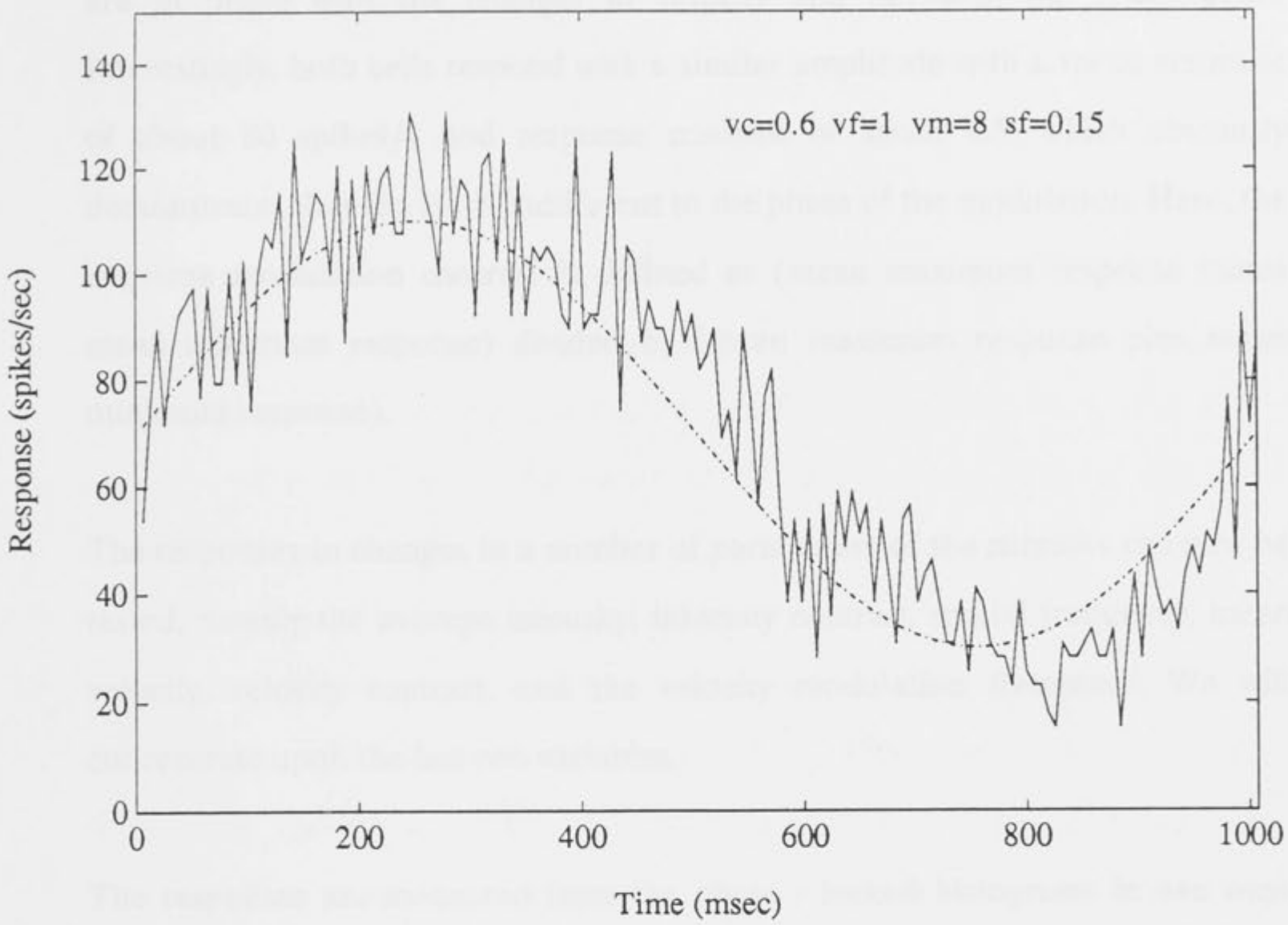
The responses of about 24 H1 neurons were recorded extracellularly in the lobula plate of the fly. The stimulus was a moving sine-wave grating of which the velocity was sinusoidally modulated. The spatial frequency ranged from 0.0376 cycles/degree to 0.376 cycles/degree, the mean angular velocity from 2 °/s to 64 °/s, the modulation contrast from 0.1 to 1.0 and the modulation frequency from 0.25 Hz to 32 Hz (see definition of these variables in this chapter). To the onset of a sine-wave grating moving at a constant velocity, the post-stimulus spike histogram response (averaged over many repetitions of the stimulus sequence) is an initial peak that decays exponentially to a plateau, as described in the previous chapter. When the motion stimulus is maintained, the averaged response is a slowly decreasing spike frequency that initially depends on the contrast frequency and the illuminance contrast of the pattern, but progressively drops to a background level that depends only on the time that has elapsed since the onset of the stimulus. So in the long term, the H1 neuron cannot give a measure of steady-state contrast frequency. We might now ask what it does measure.

5-3-1. Response modulation.

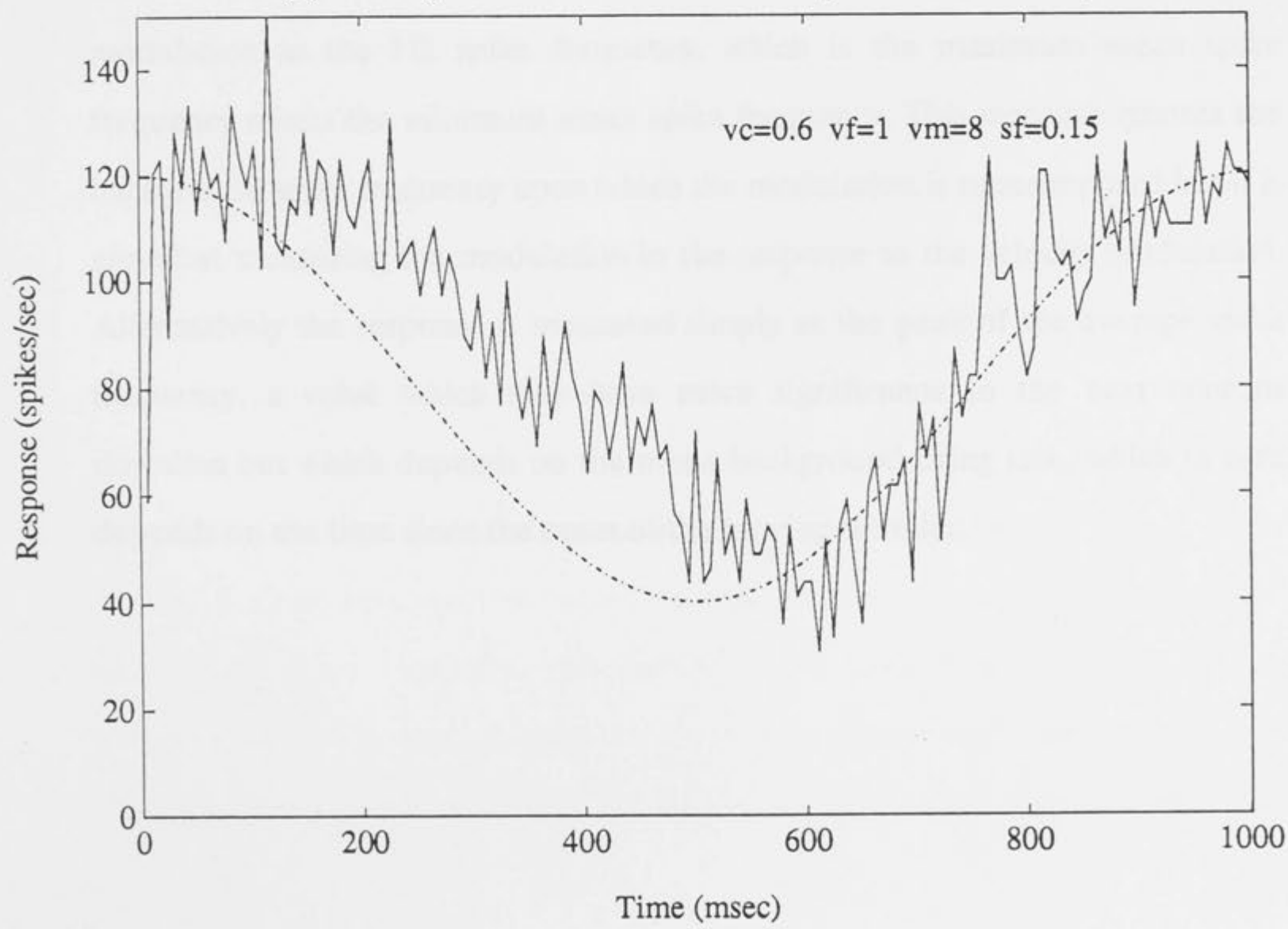
When a sine or cosine wave oscillation is added to the maintained drift of the stimulus in one direction (i.e. when the angular velocity is modulated), the response of the neuron is also sine-wave or cosine-wave modulated in phase with the modulation of the stimulus velocity. As an example, the responses of cell 24 to sinusoidally modulated velocity and the response of cell 6 to cosine-wave modulated velocity, both with mean velocity of 8 °/s, velocity modulation contrast of 0.6 and modulation frequency of 1 Hz, are shown in figure 5-1a & 5-1b, respectively. The firing frequency of cell 24 follows a beautiful sine wave

Figure 5-1. The responses of H1 to a sinusoidally modulated velocity. The stimulus pattern was a moving sine-wave grating of wavelength 6.6° and intensity contrast 0.3, its velocity was modulated either (a) sinusoidally or (b) cosinusoidally at velocity contrast 0.6 and frequency 1 Hz with mean velocity 8 °/s. An example of the sine-wave modulated response is shown in (a), which was recorded from cell 24 in response to a sinusoidally modulated velocity; the response of cell 6 to a cosinusoidally modulated velocity is shown in (b). These figures show that the firing frequency of the neurons, at the steady state, are also sine-wave (a) or cosine-wave (b) in phase with the modulation of the stimulus velocity, indicating that the responses follow the velocity change and not the velocity acceleration. Both cells had very similar response parameters, i.e, with mean response of about 80 spikes/s and response contrast of 0.5. Here, the response contrast is defined as (mean maximum response minus mean minimum response) divided by (mean maximum response plus mean minimum response).

(a) The response of H1 to a sinusoidally modulated velocity



(b) The response of H1 to a cosinusoidally modulated velocity



modulation and cell 6 displays a cosine wave, showing clearly that the responses are in phase with the changes in velocity and not with the acceleration. Interestingly, both cells respond with a similar amplitude with a mean response of about 80 spikes/s and response contrast of about 0.5, which obviously demonstrates that the H1 is indifferent to the phase of the modulation. Here, the response modulation contrast is defined as (mean maximum response minus mean minimum response) divided by (mean maximum response plus mean minimum response).

The responses to changes in a number of parameters of the stimulus can now be tested, namely the average intensity, intensity contrast, spatial frequency, mean velocity, velocity contrast, and the velocity modulation frequency. We will concentrate upon the last two variables.

The responses are measured from the phase - locked histograms in two ways because we do not know the features of the H1 response that are significant for the next neurons downline. The first measure of the response is the average modulation in the H1 spike frequency, which is the maximum mean spike frequency minus the minimum mean spike frequency. This measure ignores the background spike frequency upon which the modulation is superimposed but it is aimed at measuring the modulation in the response to the velocity modulation. Alternatively the response is measured simply as the peak of the average spike frequency, a value which may have more significance to the next neurons downline but which depends on the mean background firing rate, which in turn depends on the time since the onset of the moving stimulus.

5-3-2. Responses as a function of velocity modulation.

The effects of velocity contrast on response modulation were studied by measuring the relationship between the response contrast as well as the mean response and the velocity contrast, and by comparing the responses to sine- and cosine-wave modulations. Examples of the response modulation to various levels of velocity modulation over the range of 0 to 1.0 are plotted as raw traces in figure 5-2a, which shows the recorded from cell 12 with a mean velocity of 10 °/s and a velocity modulation frequency of 1 Hz. The responses of cell 5 to cosinusoidally modulated velocity with a modulation frequency of 1 Hz and a mean velocity of 6 °/s are shown in figure 5-2b. In both cases, the cells exhibit a wonderful performance of faithfully following the velocity modulation for almost the whole range of velocity contrast from 0.2 to 1, and even at a very low contrast of 0.1 the oscillation in the firing frequency which records the velocity modulation has already appeared. This observation shows that the response of the H1 neuron, in terms of its modulation contrast, can be considered as a copy of the velocity modulation of stimulus, and that the neuron is capable of accurately following the velocity changes in a continued movement. The responses are delayed about 50 ms after the onset of stimulus, and this time is much longer than the delay time observed from the transient response, in which it is usually around 20 ms. The response to an extra movement in the steady state is not so fast as to the initial transient, implying a variability of the temporal constants in the fly's motion-detection system.

Direct evidence for the neuron measuring the velocity contrast comes from plotting the response contrast versus the velocity contrast for different levels of velocity. As velocity contrast increases from 0.1 to 1.0 the response contrast correspondingly increases linearly to 1.0, irrespective of the mean velocity and the velocity modulation (figure 5-3). For the mean velocities ranging from 4 °/s

Figure 5-2. Records of the responses to sinusoidally or cosinsoidally modulated angular velocity at different velocity contrasts. (a) The responses of cell 12 to velocity contrast ranging from 0 to 0.95 at mean velocity 10 °/s. (b) The responses of cell 5 to a cosinusoidally modulated velocity with the velocity contrast from 0 to 1.0 at mean velocity 6 °/s. The vertical axis is the average spike firing frequency over 50 repetitions; the horizontal axis is phase-locked to the velocity modulation frequency of 1 Hz, making each record 1 second long; the period of the stimulus grating was still 6.6°. As the velocity modulation contrast increased, the cells followed the velocity modulation very well, at least, for the range of velocity contrast from 0.2 to 0.95. Even to the stimulus with a very low contrast of 0.1, the neuron was still able to generate a response with noticeable modulation. At the velocity contrast of 1, however, which means that the speed was 0 °/s at phase 180° for the cosinusoidal modulation, the response modulation was distorted.

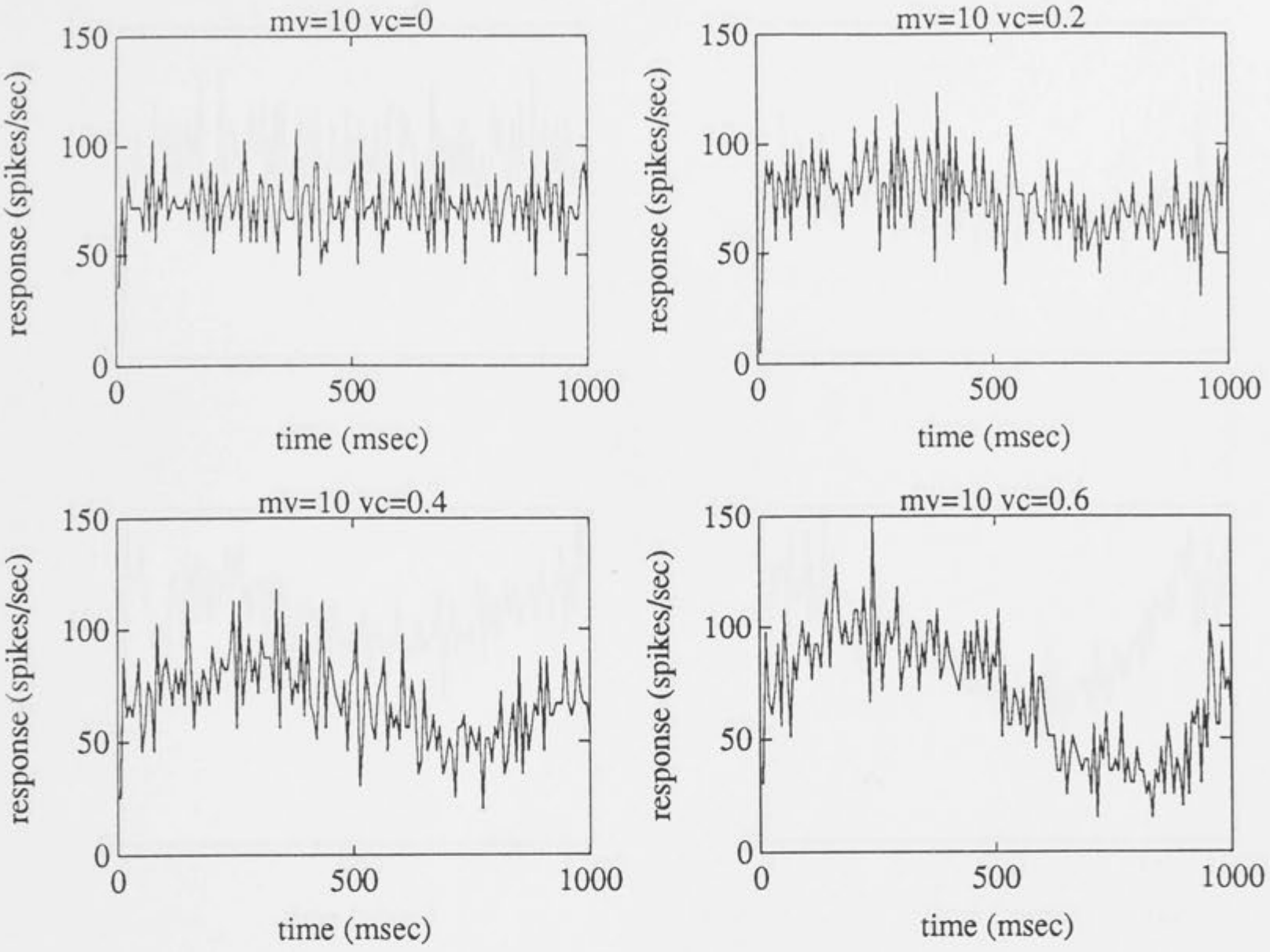

mv=10 vc=0
mv=10 vc=0.2
mv=10 vc=0.4
mv=10 vc=0.6
response (spikes/sec)
time (msec)
0
50
100
150
500
1000

Fig. 5-2a

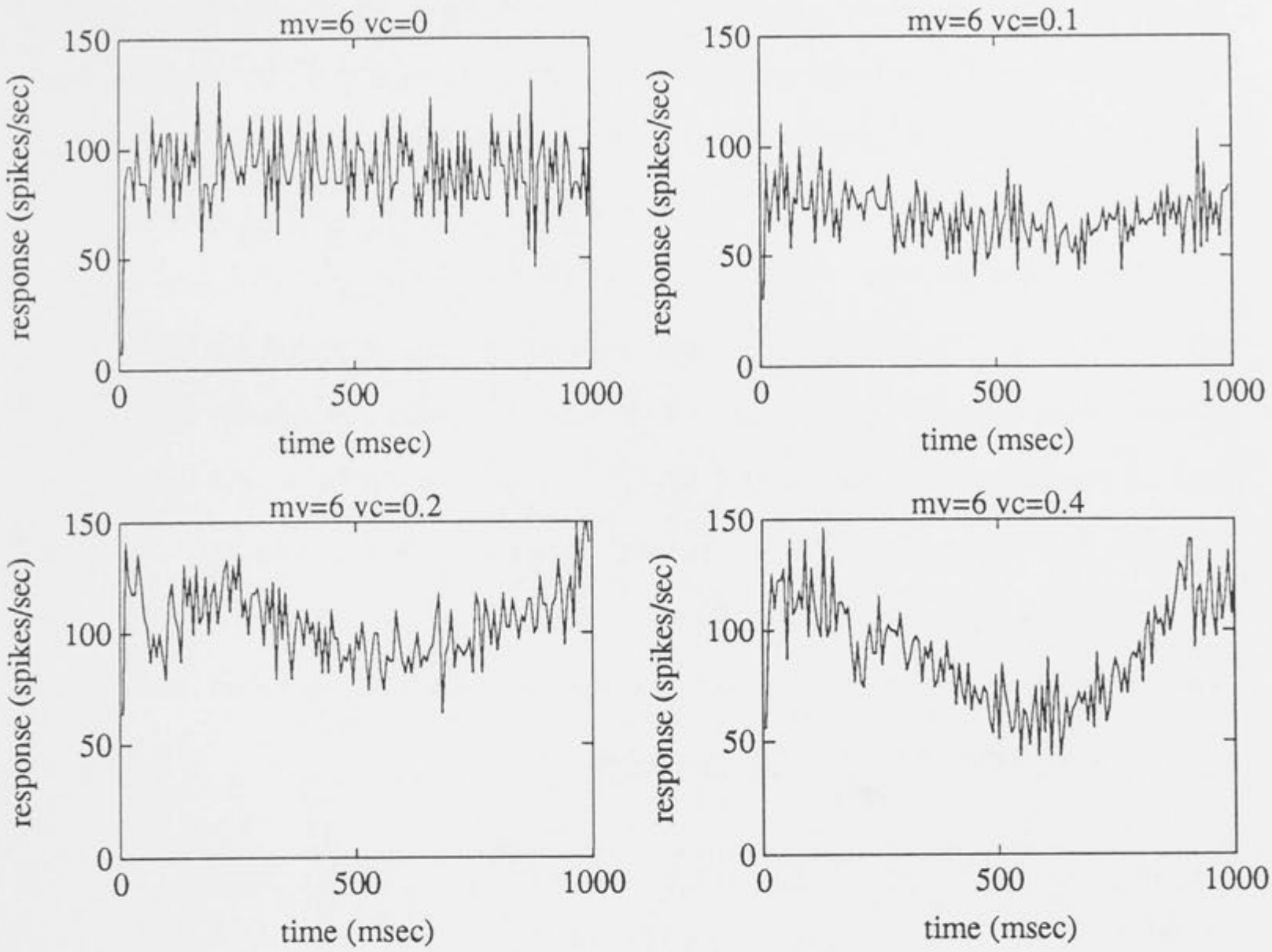
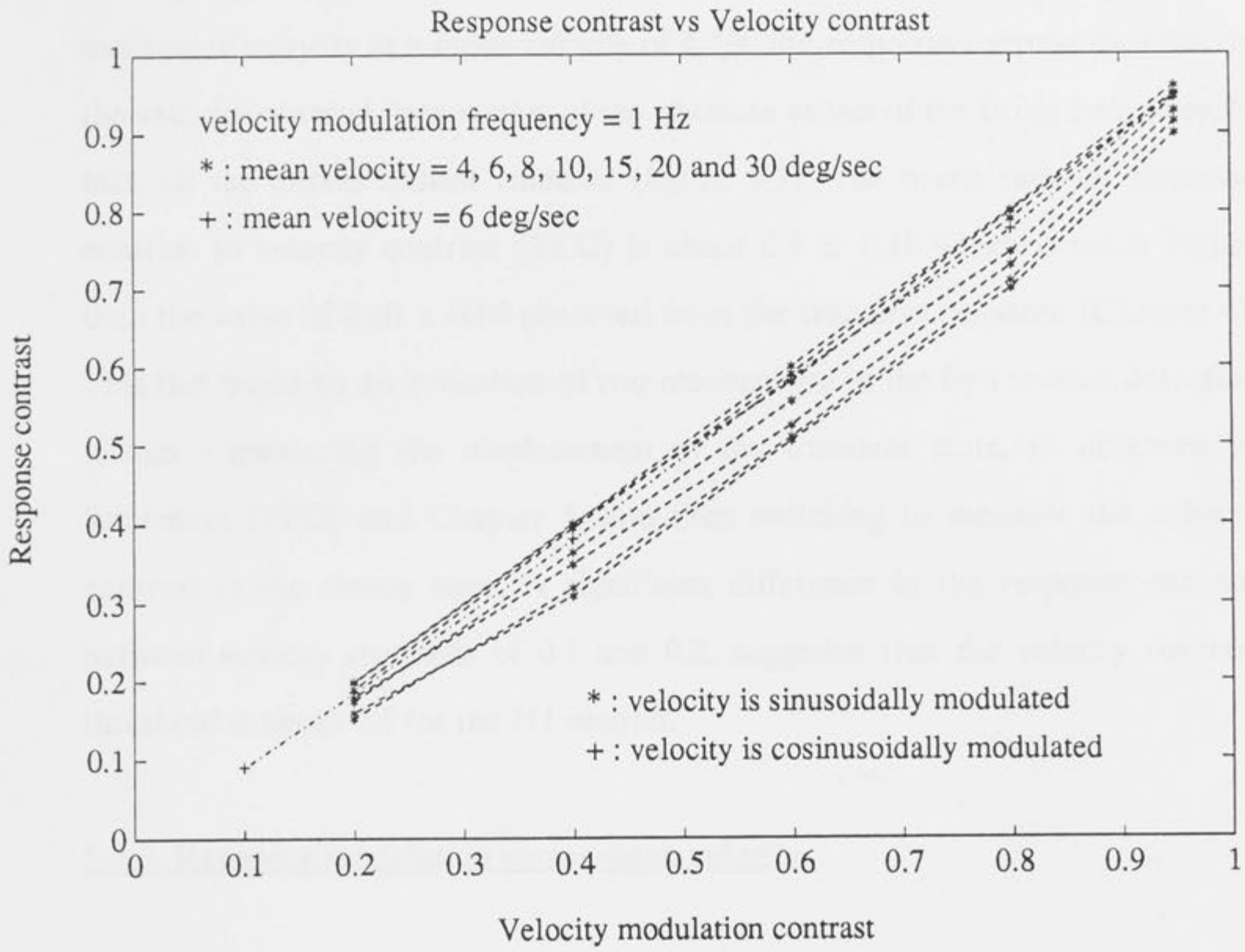

mv=6 vc=0
mv=6 vc=0.1
mv=6 vc=0.2
mv=6 vc=0.4
mv=6 vc=0.6
mv=6 vc=0.8
mv=6 vc=1
response (spikes/sec)
time (msec)
0
50
100
150
500
1000

Fig. 5-2b

Figure 5-3. The response contrast is linearly dependent on the stimulus velocity contrast, irrespective of mean velocity. The experiments were done on cell 12, which was stimulated by a sinusoidally modulated mean velocity ranging from 4 °/s to 30 °/s as indicated, with modulation frequency 1 Hz; and on cell 5 with a cosinusoidally modulated mean velocity of 6 °/s and modulation frequency 1 Hz. As velocity contrast increased from 0.1 to 0.95, the response contrast increased linearly for all stimuli, irrespective of other factors. This result is apparently coincident with the finding that the neuron can respond to the velocity up to 50 °/s in the steady state (Chapter 4). The average ratio of response contrast to velocity contrast was 0.9 ± 0.10, which is much higher than that the value of 0.6 ± 0.10 obtained from the transient response (Chapter 4), suggesting that the neuron is very well adapted to response to velocity contrast in the steady state.


Response contrast vs Velocity contrast
velocity modulation frequency = 1 Hz
* : mean velocity = 4, 6, 8, 10, 15, 20 and 30 deg/sec
+ : mean velocity = 6 deg/sec
* : velocity is sinusoidally modulated
+ : velocity is cosinusoidally modulated
Response contrast
Velocity modulation contrast
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1

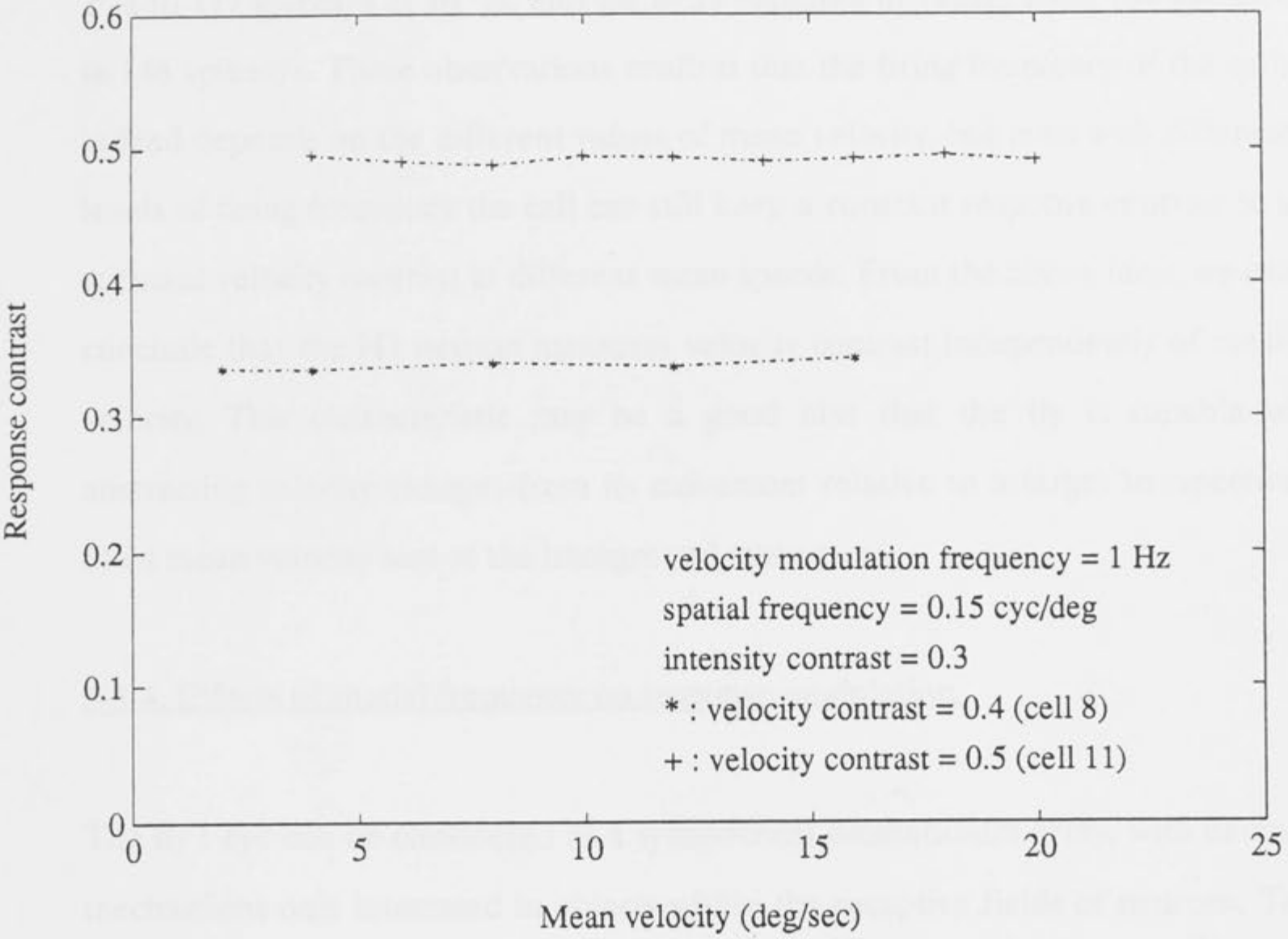
to 30 °/s, on cell 12 with sinusoidal velocity modulation, as well as cosine-wave modulated velocity at a mean velocity of 6 °/s, the response contrast depends on the velocity contrast irrespective of the absolute values of the firing frequency. In fact, all the curves almost coincide (figure 5-3). The mean ratio of response contrast to velocity contrast (RCC) is about 0.9 ± 0.10 which is much higher than the value of 0.60 ± 0.09 observed from the transient response (Chapter 4). This fact might be an indication of two mechanisms in the fly's motion detection system - measuring the displacement at the transient state, as observed by Srinivasan (1983) and Chapter 3, and then switching to measure the velocity contrast in the steady state. A significant difference in the response contrast between velocity contrasts of 0.1 and 0.2, suggestes that the velocity contrast threshold is about 0.1 for the H1 neuron.

5-3-3. Response modulation versus mean velocity.

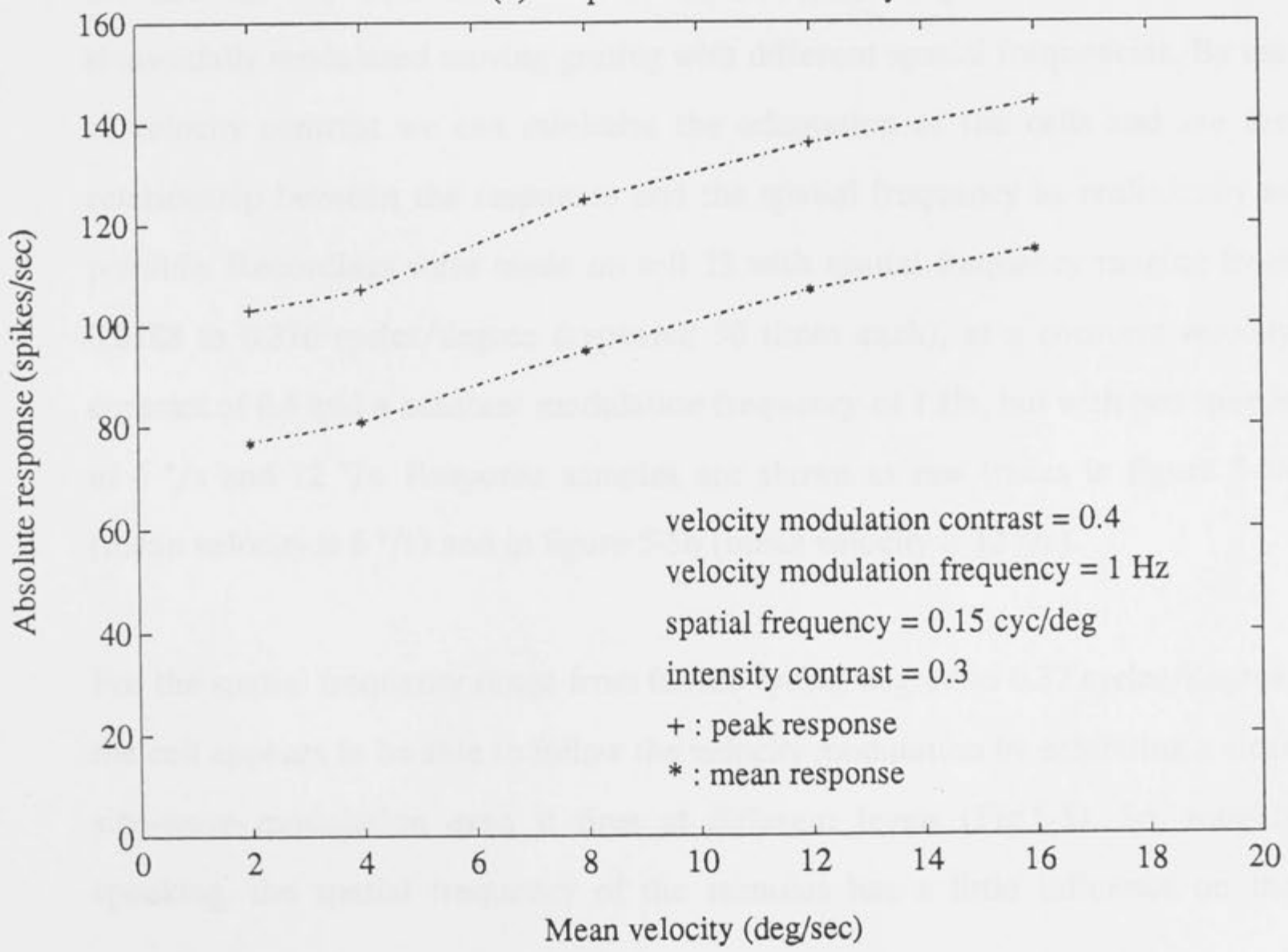
To investigate the relationship between the response contrast and the mean velocities in more detail, the recordings were done on two other cells - cell 8 responding only to velocity modulation contrast of 0.4 and 0.0 with mean velocities ranging from 2 °/s to 16 °/s and cell 11 stimulated by the same pattern but with velocity contrast of 0.5 and mean velocities from 4 °/s to 20 °/s. The curves of response contrast versus mean velocity are plotted in figure 5-4. The mean response and the peak response of cell 8 versus the mean velocity are also plotted in Fig. 5-4 for comparison. The response contrast keeps almost constant while the mean response and peak response increasing nonlinearly, as mean velocity increases from 2 °/s to 20 °/s. The mean response contrast is 0.345 for movements of velocity contrast 0.4 and is 0.49 at a velocity contrast of 0.5. The mean ratio of response contrast to velocity contrast is 0.86 in response to a velocity contrast of 0.4, and rises to nearly 0.98 when the velocity contrast is 0.5. The mean response of cell 8 increases from 80 spikes/s at a mean velocity of

Figure 5-4. Further demonstration of the response to velocity contrast irrespective of the mean velocity. The responses of Cell 8 and cell 11 to the sinusoidally modulated movements are plotted against the mean velocities. The stimulus was a sine-wave grating of spatial frequency 0.15 cyc/deg and intensity contrast 0.3; the speed was sinusoidally modulated at a frequency of 1 Hz and contrast 0.4 or 0.5, with the mean velocity controlled from 2 °/s to 20 °/s. (a) The response contrast remained almost constant for all this range, with a value of about 0.49 for velocity contrast 0.5, and about 0.345 at a velocity contrast of 0.4, demonstrating clearly that the cells respond to velocity contrast, irrespective of the mean velocity. (b) However, the cells responded differently to the different mean velocities in terms of the absolute spike firing frequency. The peak response and the mean response both increased monotonically as the mean velocity increased.

(a) Response contrast vs Mean velocity



(b) Response vs Mean velocity



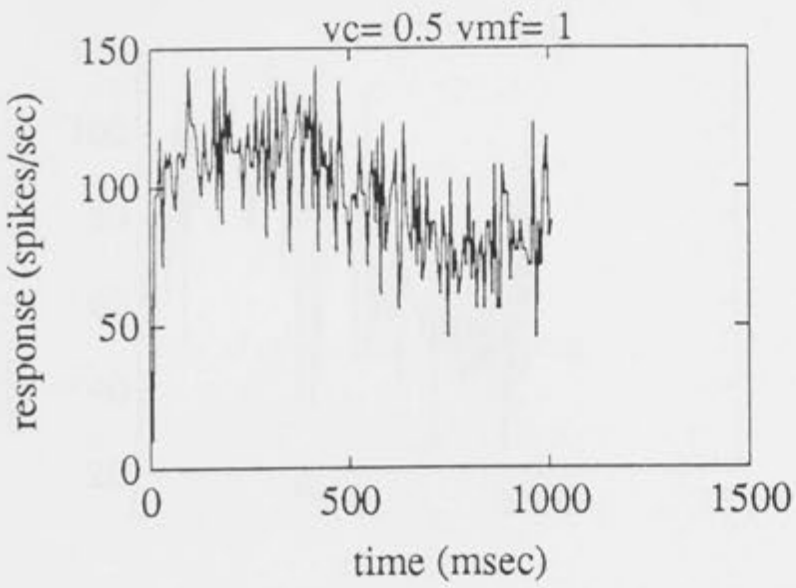
2°/s to 117 spikes/s at 16 °/s, and the peak response increases from 104 spikes/s to 146 spikes/s. These observations confirm that the firing frequency of the cells indeed depends on the different values of mean velocity, but even with different levels of firing frequency the cell can still keep a constant response contrast to a constant velocity contrast at different mean speeds. From the above facts, we can conclude that the H1 neuron measures velocity contrast independently of mean velocity. This characteristic may be a good hint that the fly is capable of abstracting velocity changes from its movement relative to a target irrespective of its mean velocity and of the background movement.

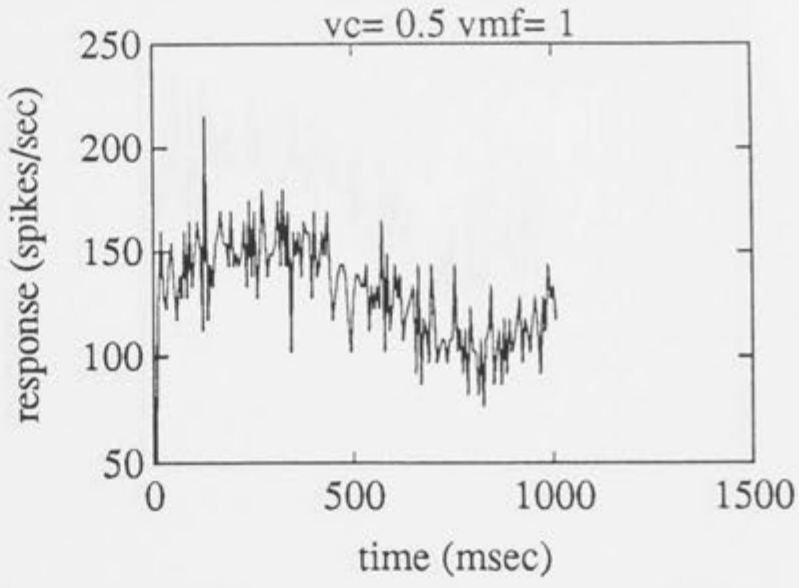
5-3-4. Effects of spatial frequency on response modulation.

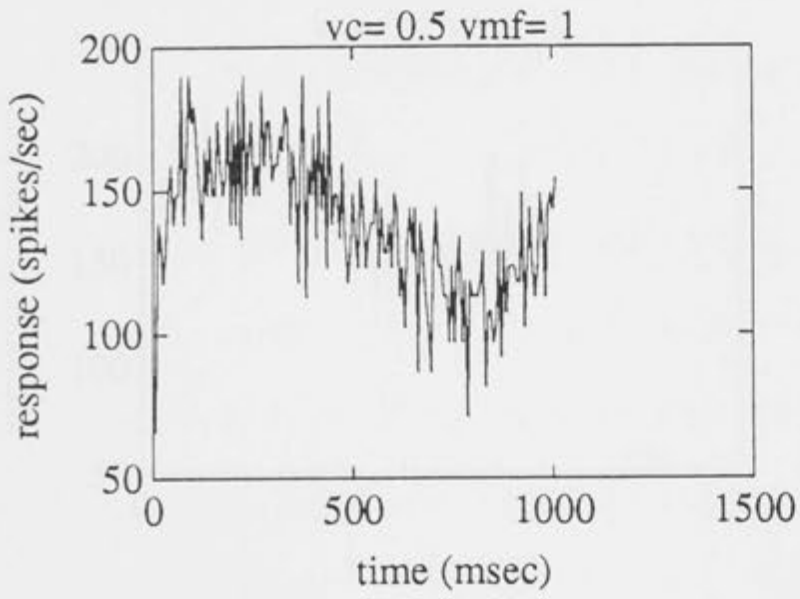
The fly's eye can be considered as a symmetrical ommatidium array, with neural mechanisms only interested in objects within the receptive fields of neurons. To determine the influence of the stimulus spatial structure on the response of the H1 neuron, the best kind of stimulus for simulating natural scenes is a sinusoidally modulated moving grating with different spatial frequencies. By use of velocity contrast we can minimize the adaptation of the cells and see the relationship between the responses and the spatial frequency as realistically as possible. Recordings were made on cell 13 with spatial frequency ranging from 0.0188 to 0.376 cycles/degree (repeated 30 times each), at a constant velocity contrast of 0.4 and a constant modulation frequency of 1 Hz, but with two speeds of 6 °/s and 12 °/s. Response samples are shown as raw traces in figure 5-5a (mean velocity is 6 °/s) and in figure 5-5b (mean velocity is 12 °/s).

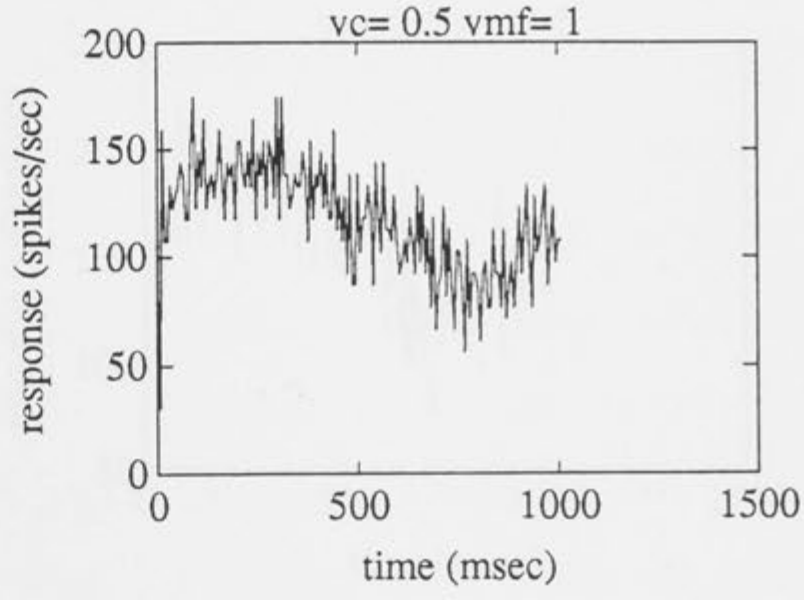
For the spatial frequency range from 0.0188 cycles/degree to 0.37 cycles/degree, the cell appears to be able to follow the velocity modulation by exhibiting a clear sine-wave modulation even it fires at different levels (Fig.5-5). So, roughly speaking, the spatial frequency of the stimulus has a little influence on the

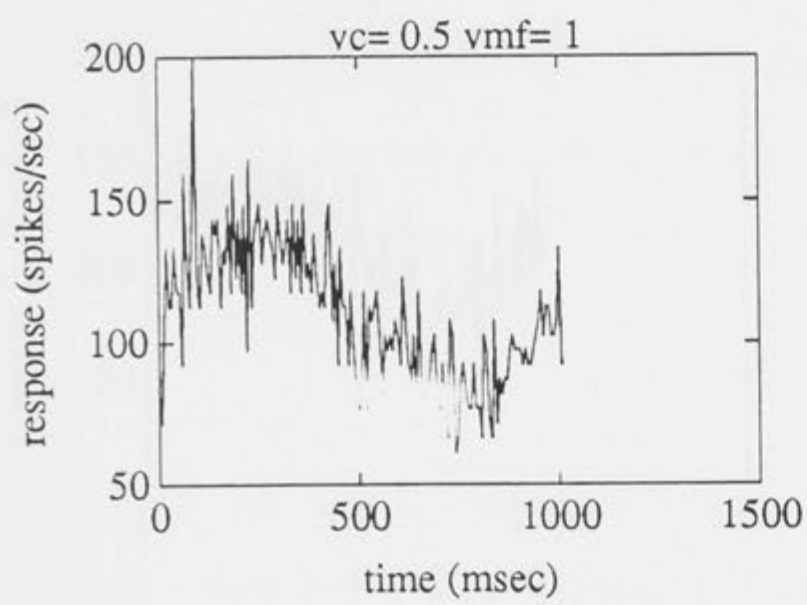
Figure 5-5. The influence of spatial frequency on the response. A sine-wave grating with spatial frequencies ranging from 0.0376 cyc/deg to 0.3764 cyc/deg in 7 steps was used as the stimulus pattern. It moved at two mean angular velocities 6 °/s and 12 °/s, with velocity contrast 0.4 and modulation frequency 1 Hz. Records are from a H1 neuron - cell 13, (a) with mean velocity 6 °/s and (b) with mean velocity 12 °/s. As the spatial frequency increases from 0.037 cyc/deg to 0.37 cyc/deg, the responses oscillate in a beautiful sine wave. Once again the mean velocity has no influence on the response modulation. Spatial frequency has an effect on the response strength and also increased the noise in the responses at low and at high spatial frequencies (for example 0.37 cyc/deg in (b)). The neuron gave its best response to middle spatial frequencies (for example 0.11 cyc/deg and 0.15 cyc/deg in the second row) with high response strength and clear modulation.

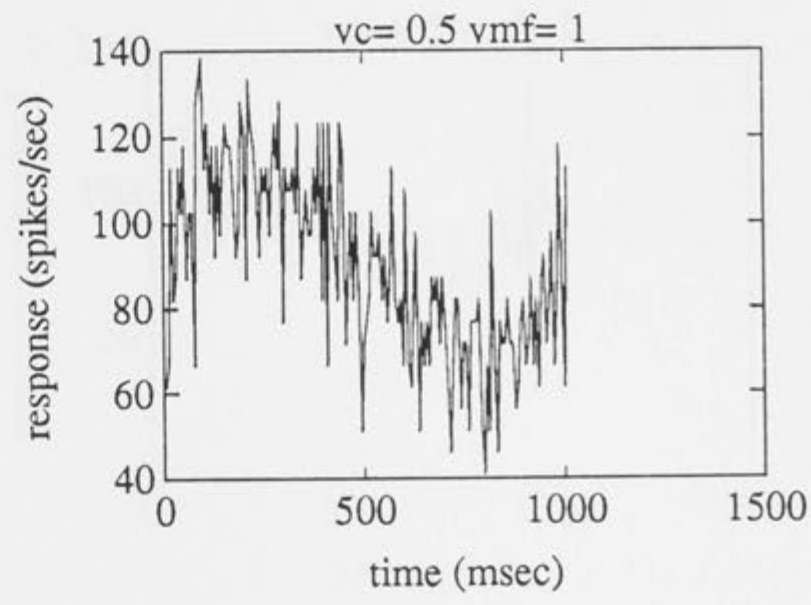

vc= 0.5 vmf= 1
response (spikes/sec)
time (msec)
0
50
100
150
0
500
1000
1500

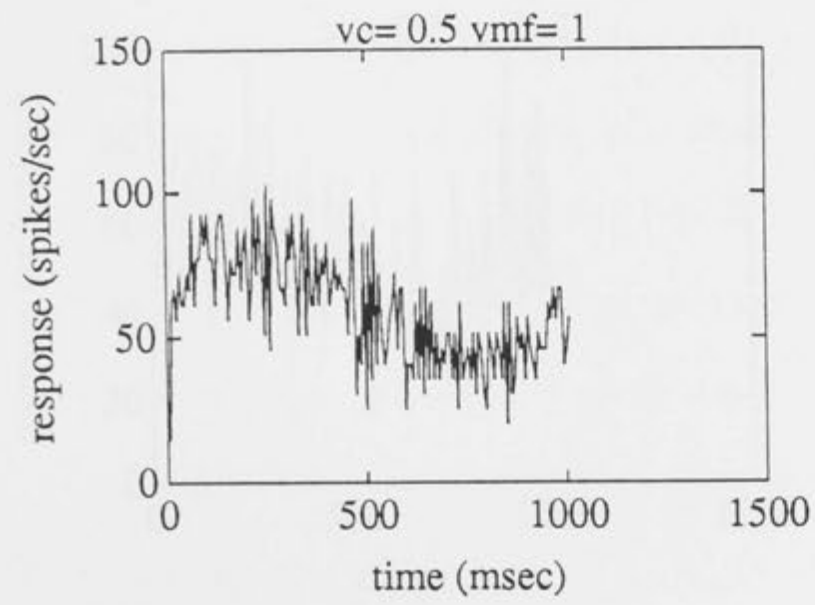

vc= 0.5 vmf= 1
response (spikes/sec)
time (msec)
50
100
150
200
250
0
500
1000
1500


vc= 0.5 vmf= 1
response (spikes/sec)
time (msec)
50
100
150
200
0
500
1000
1500


vc= 0.5 vmf= 1
response (spikes/sec)
time (msec)
0
50
100
150
200
0
500
1000
1500


vc= 0.5 vmf= 1
response (spikes/sec)
time (msec)
50
100
150
200
0
500
1000
1500


vc= 0.5 vmf= 1
response (spikes/sec)
time (msec)
40
60
80
100
120
140
0
500
1000
1500


vc= 0.5 vmf= 1
response (spikes/sec)
time (msec)
0
50
100
150
0
500
1000
1500

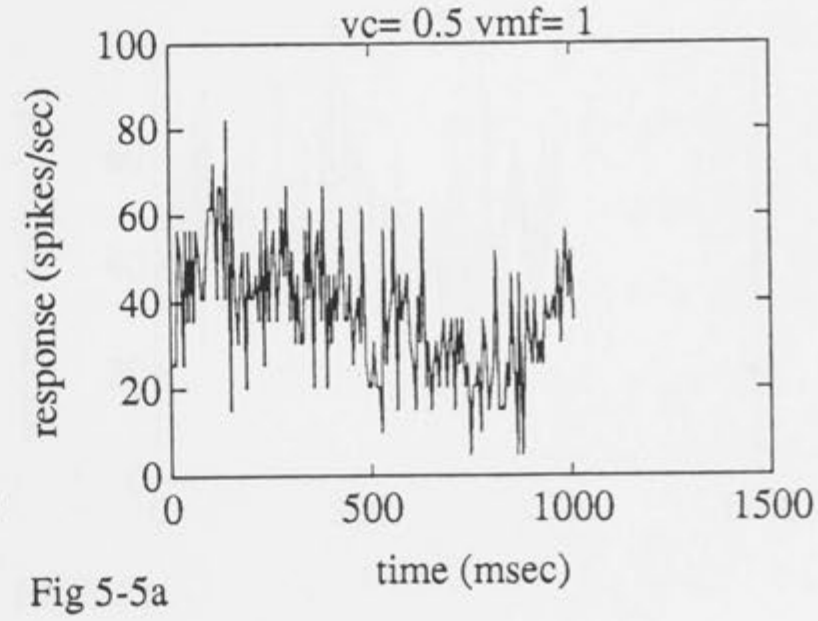

vc= 0.5 vmf= 1
response (spikes/sec)
time (msec)
0
20
40
60
80
100
0
500
1000
1500

Fig 5-5a

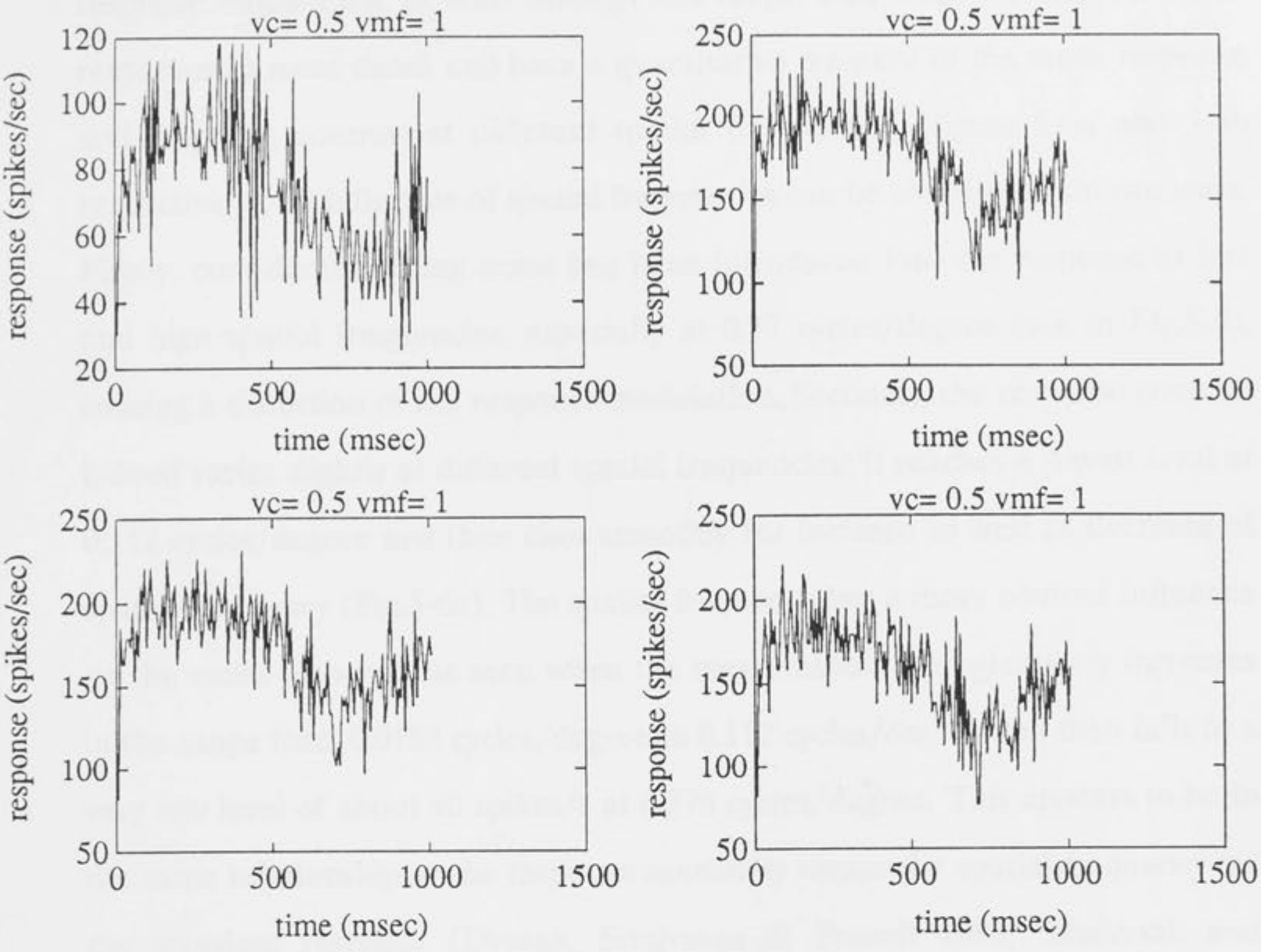

vc= 0.5 vmf= 1
response (spikes/sec)
time (msec)
vc= 0.5 vmf= 1
response (spikes/sec)
time (msec)
vc= 0.5 vmf= 1
response (spikes/sec)
time (msec)
vc= 0.5 vmf= 1
response (spikes/sec)
time (msec)
vc= 0.5 vmf= 1
response (spikes/sec)
time (msec)
vc= 0.5 vmf= 1
response (spikes/sec)
time (msec)
vc= 0.5 vmf= 1
response (spikes/sec)
time (msec)
vc= 0.5 vmf= 1
response (spikes/sec)
time (msec)

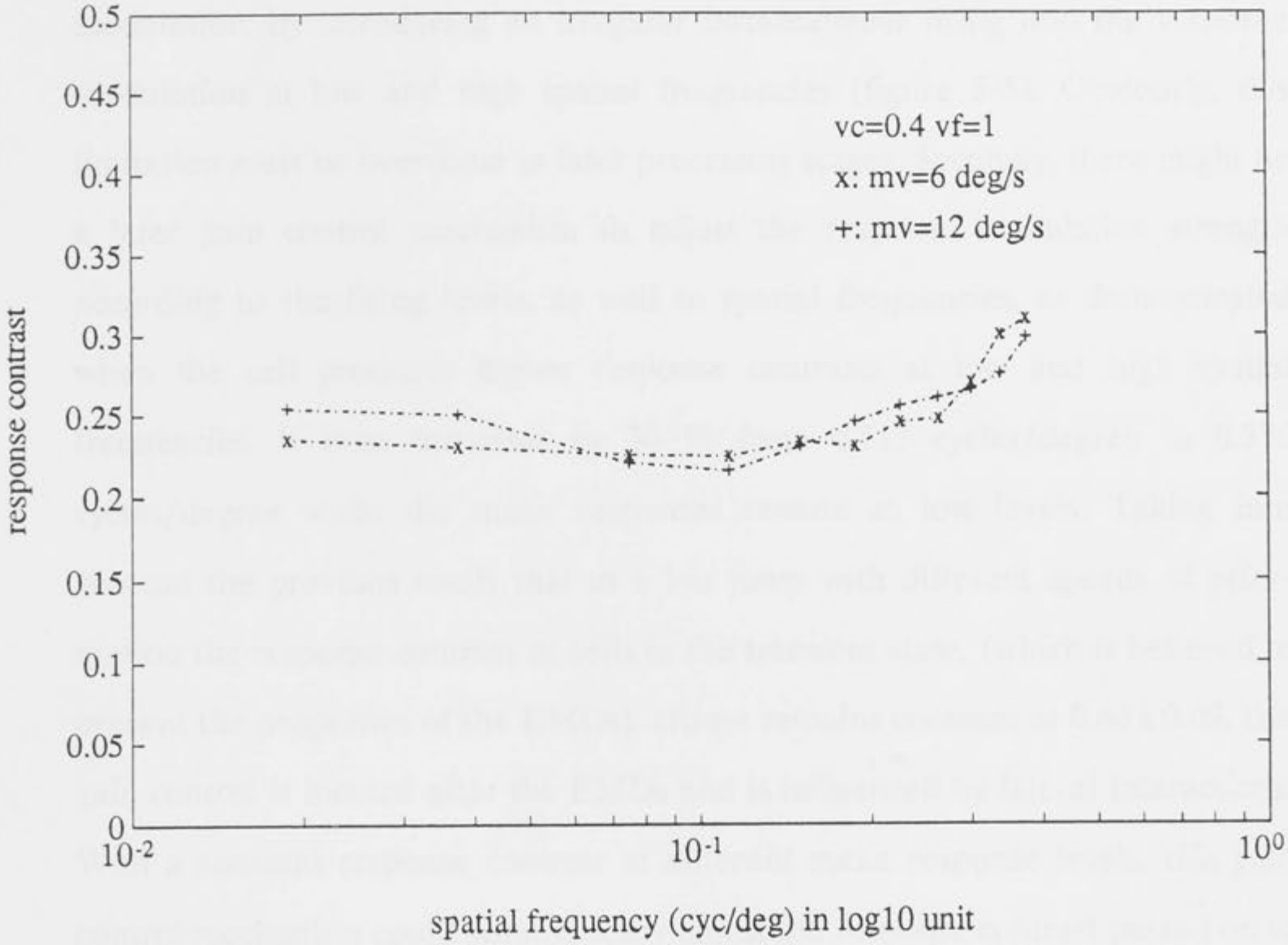
Fig 5-5b

response modulation, at least through this range. But, when we examine these responses in more detail and have a quantitative measure of the mean response and response contrast at different spatial frequencies, (figure 5-6a and 5-6b respectively), an influence of spatial frequencies can be clearly seen in two ways. Firstly, considerable firing noise has been introduced into the response at low and high spatial frequencies, especially at 0.37 cycles/degree (see in Fig.5-5), causing a distortion of the response modulation. Secondly, the response contrast indeed varies slightly at different spatial frequencies; it reaches a lowest level at 0.112 cycles/degree and then rises smoothly for increase as well as decrease of spatial frequency (Fig.5-6a). The spatial frequency has a more obvious influence on the mean response, as seen when the mean response progressively increases in the range from 0.0188 cycles/degree to 0.112 cycles/degree and then falls to a very low level of about 40 spikes/s at 0.376 cycles/degree. This appears to be in the same relationship as the response sensitivity versus the spatial frequency for the transient response (Dvorak, Srinivasan & French 1980; Srinivasan and Dvorak 1980). Over this frequency range the mean velocity has no influence on the response contrast but it does affect the mean response, as demonstrated by comparing the two groups of curves at two speeds in figure 5-6, in which the two response contrast curves are close together but the two mean response curves are separated.

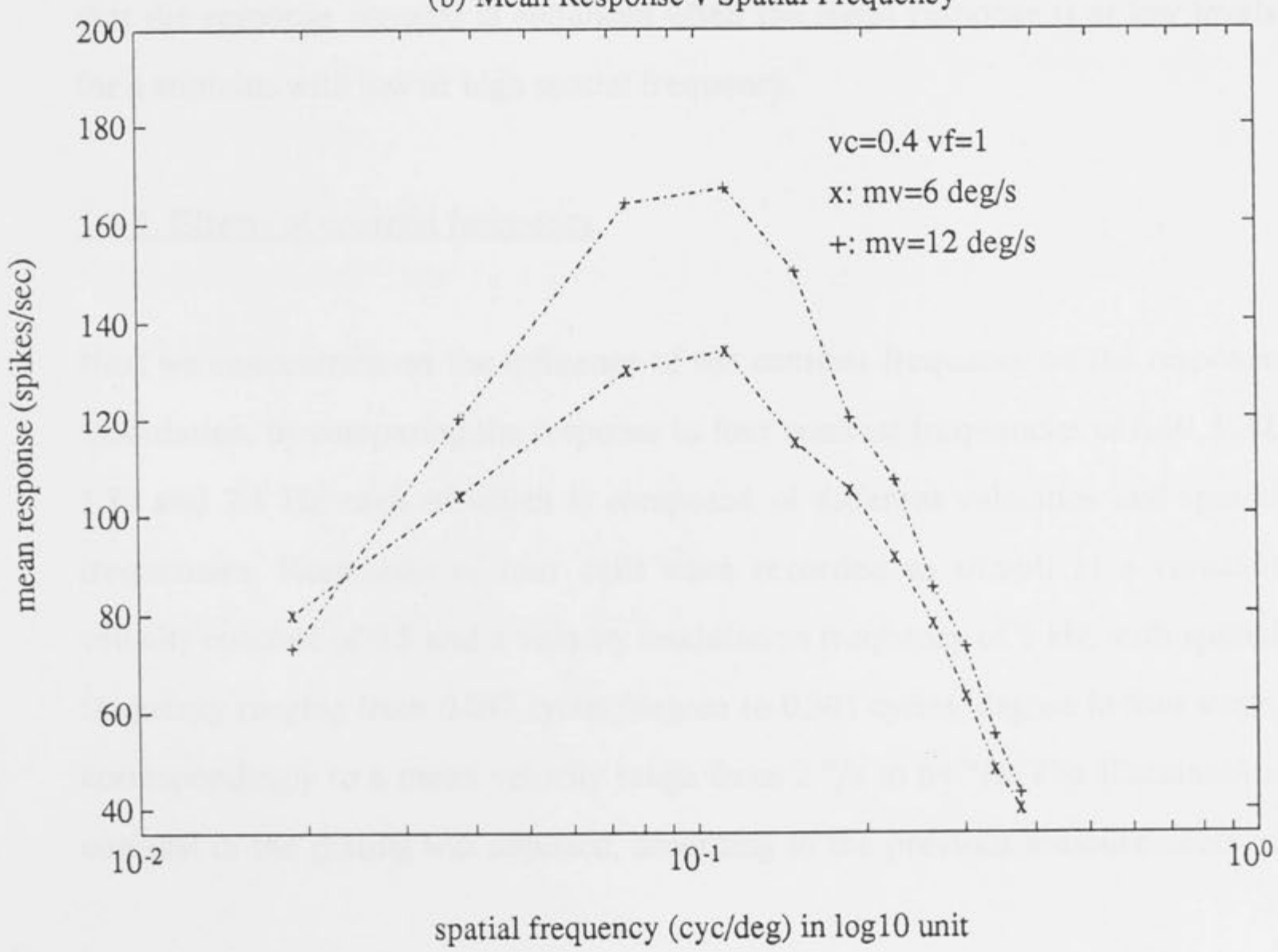
From the above observations, some conclusions can be suggested: Firstly, the fly's eyes in functional terms can be represented as a band-pass spatial filter with the centre position at about 0.113 cycles/degree and upper limit (75%) at 0.376 cycles/degree, since the H1 neurons have a bell-shaped response sensitivity when plotted against the spatial frequency. This spatial filtering might be a product of the ommatidia possessing a certain range of receptive field or of lateral interactions between the EMDs, because both effects can effectively force a cell to have a peak sensitivity at certain spatial frequencies. We also

Figure 5-6. Response modulation contrast as a function of spatial frequency (cell 13). The stimulus was a sine-wave grating of wavelength 6.6°, with velocity contrast 0.4, velocity modulation frequency 1 Hz, and mean velocities 6 °/s (+) and 12 °/s (x). (a) The response contrast is plotted against spatial frequency and (b) the mean response versus spatial frequency. (a) When spatial frequency increased from 0.037 cyc/deg to 0.37 cyc/deg in ten steps, the response contrast slightly decreased from 0.25 to 0.225 at 0.112 cyc/deg, and then increased to about 0.3 at 0.37 cyc/deg. This result suggests a mechanism which controls the response contrast strength in such a way that if mean response is reduced the response contrast will increase. Comparing (a) and (b), the mean response decreases as the response contrast increases. As seen in (b), the larger-field motion detection neurons act as spatial band-pass filters with peak near a pattern period of 10°.

(a) Response Modulation v Spatial Frequency



(b) Mean Response v Spatial Frequency



observe that this filter distorts the ability of the cells to measure velocity modulation, by introducing an irregular instantaneous firing into the response modulation at low and high spatial frequencies (figure 5-5). Obviously, this limitation must be overcome in later processing stages. Secondly, there might be a later gain control mechanism to adjust the response modulation strength according to the firing levels, as well to spatial frequencies, as demonstrated when the cell produces higher response contrasts at low and high spatial frequencies. It even increases by 30 % from 0.113 cycles/degree to 0.376 cycles/degree while the mean responses remain at low levels. Taking into account the previous result that to a bar jump with different speeds of prior-motion the response contrast of cells in the transient state, (which is believed to present the properties of the EMDs), always remains constant at 0.60 ± 0.09, this gain control is located after the EMDs and is influenced by lateral interactions. With a constant response contrast at different mean response levels, this gain control mechanism could automatically adjust the response contrast passed on to the next stages according to mean response levels and lateral interactions, so that the response contrast is enhanced when the mean response is at low levels for a stimulus with low or high spatial frequency.

5-3-5. Effects of contrast frequency.

Next we concentrate on the influence of the contrast frequency on the response modulation, by comparing the response to four contrast frequencies of 0.60, 1.20, 1.80 and 2.4 Hz each of which is composed of different velocities and spatial frequencies. Responses of four cells were recorded to stimuli at a constant velocity contrast of 0.5 and a velocity modulation frequency of 1 Hz, with spatial frequency ranging from 0.037 cycles/degree to 0.301 cycles/degree in four steps, correspondingly to a mean velocity range from 2 °/s to 64 °/s. The illumination contrast of the grating was adjusted, according to the previous measurements of

contrast sensitivity versus spatial frequency in the H1 neuron (Srinivansn and Dvorak 1980), to compensate for the loss of stimulus intensity at the receptor level. An example of the responses of cell 16, plotted in figure 5-7a, shows that the neuron can faithfully follow the velocity modulation for all these contrast frequencies but the response strengths are independent on the contrast frequency.

When the response contrast is plotted against the contrast frequency, in the upper part of figures 5-7b, the contrast frequency has a significant influence on the response contrast. All four cells produce an almost constant response contrast to four spatial frequencies or four speeds irrespective of quadrupling the contrast frequency. There are also difference in the response contrast to the stimuli at a constant contrast frequency but with different combinations of spatial frequency and velocity. Normally, the response contrasts to a spatial frequency of 0.075 cycles/degree are at the lowest levels and those to 0.301 cycles/degree are at the highest levels. From these phenomena it can be concluded that the contrast frequency only slightly affects the response modulation. In the other words, the H1 neuron does not measure contrast frequency, at least at its steady state, in the way that it measures velocity modulation. To stimuli of constant contrast frequency it can respond with different amplitudes, and to different contrast frequencies it may respond with the same modulation.

When we look at the relationship between the mean response and the contrast frequency, plotted in the bottom of figures 5-7b, effects of contrast frequency are more apparent. With contrast frequency increasing, commonly, the mean responses also slowly increase, although the responses to one contrast frequency also vary at different mean levels according to the spatial frequencies. The mean responses reach the highest level when the spatial frequency is 0.075

Figure 5-7a. The responses of cell 16 at different contrast frequencies. The stimulus was a sine-wave grating, with the velocity sinusoidally-modulated at a constant velocity contrast 0.5 and modulation frequency 1 Hz. Four contrast frequencies were used - 0.6, 1.2, 1.8 and 2.4 cyc/s, each of which was produced by four combinations of mean velocity and spatial frequency. For example, a contrast frequency of 0.6 cyc/s was reached by multiplying the following spatial frequency with mean velocity, 0.3 cyc/deg with 2 deg/s, 0.15 cyc/deg with 4 deg/s, 0.075 cyc/deg with 8 deg/s, and 0.0375 cyc/deg with 16 deg/s. Obviously, to all the four contrast frequencies, the cell can faithfully catch the velocity modulation, exhibiting a beautiful sine-wave oscillation in the spike firing frequency. The response contrast and the mean response were independent of the contrast frequency, but there was a big difference between the responses which were generated by just one contrast frequency at four different mean velocity and spatial frequency combinations. In fact, the cell always produced a strong response to the combination with fast speed and low spatial frequency. The dashdot lines present the relative zero base line.

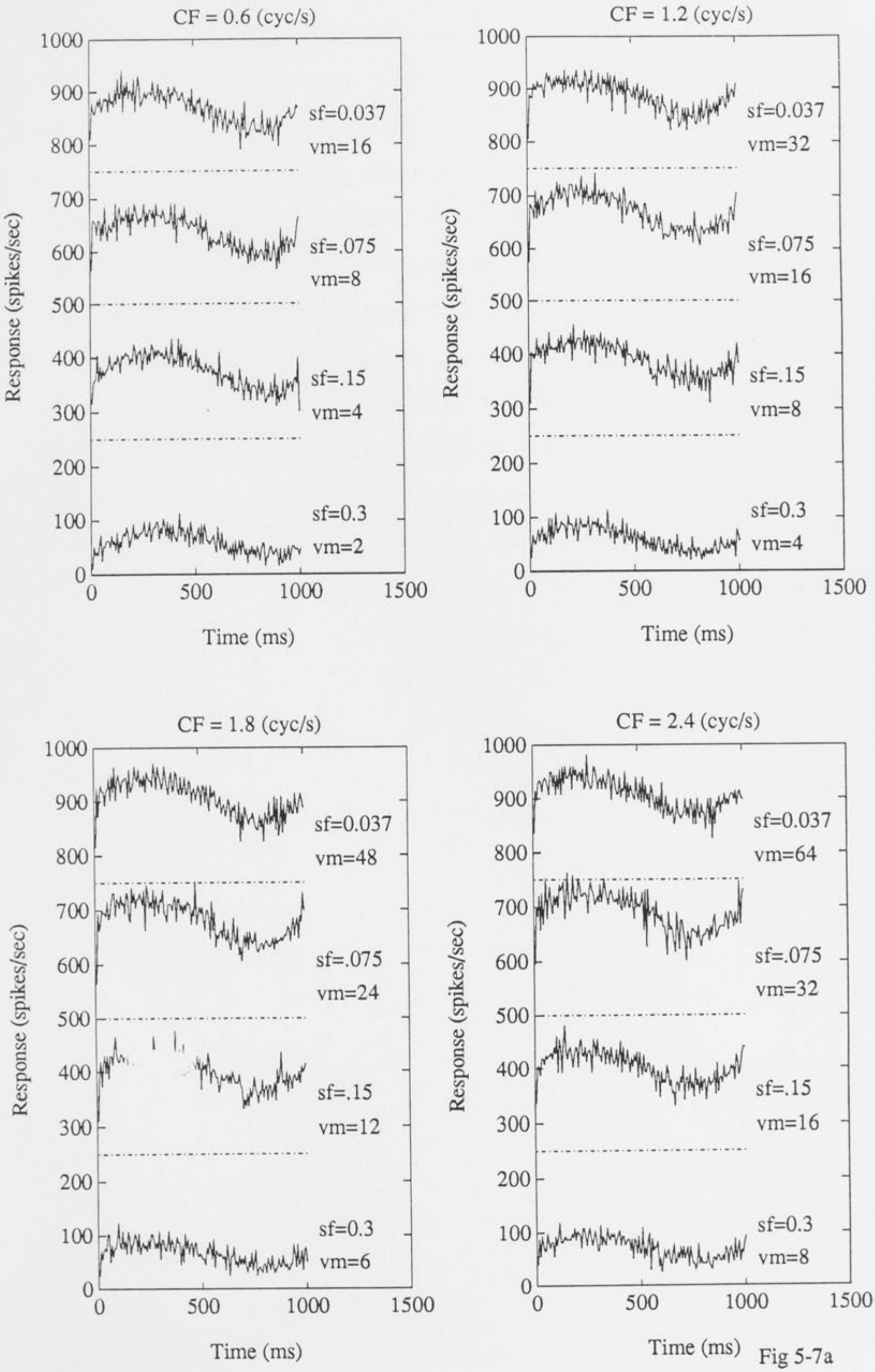

CF = 0.6 (cyc/s)
CF = 1.2 (cyc/s)
CF = 1.8 (cyc/s)
CF = 2.4 (cyc/s)
Response (spikes/sec)
Time (ms)
sf=0.037
vm=16
sf=.075
vm=8
sf=.15
vm=4
sf=0.3
vm=2
sf=0.037
vm=32
sf=.075
vm=16
sf=.15
vm=8
sf=0.3
vm=4
sf=0.037
vm=48
sf=.075
vm=24
sf=.15
vm=12
sf=0.3
vm=6
sf=0.037
vm=64
sf=.075
vm=32
sf=.15
vm=16
sf=0.3
vm=8
0
100
200
300
400
500
600
700
800
900
1000
0
500
1000
1500

Fig 5-7a

Figure 5-7b. Quantitative relationships between the contrast frequency and the response contrast as well as the mean response of four cells. The data were obtained from cell 16, cell 20, cell 21, and cell 22. The stimulation was as in Fig. 5-7a. The response contrast versus the contrast frequency is plotted in the upper part of the figure, and the curves of the mean response against the contrast frequency are shown in the lower part of the figure. The symbol "*" presents a spatial frequency of 0.301 cyc/deg, "o", "+", and "x" present the spatial frequencies of 0.15 cyc/deg, 0.075 cyc/deg, and 0.037 cyc/deg, respectively. Comparing these four cells, the stimulus contrast frequency has little influence on the response contrast over this range of frequency. Four different strengths of the response contrast can be generated by the stimulus at one contrast frequency, or the response contrasts can be the same at four contrast frequencies. However, the stimulus contrast frequency has a small effect on the mean response in that the faster the contrast frequency, the stronger the mean response.

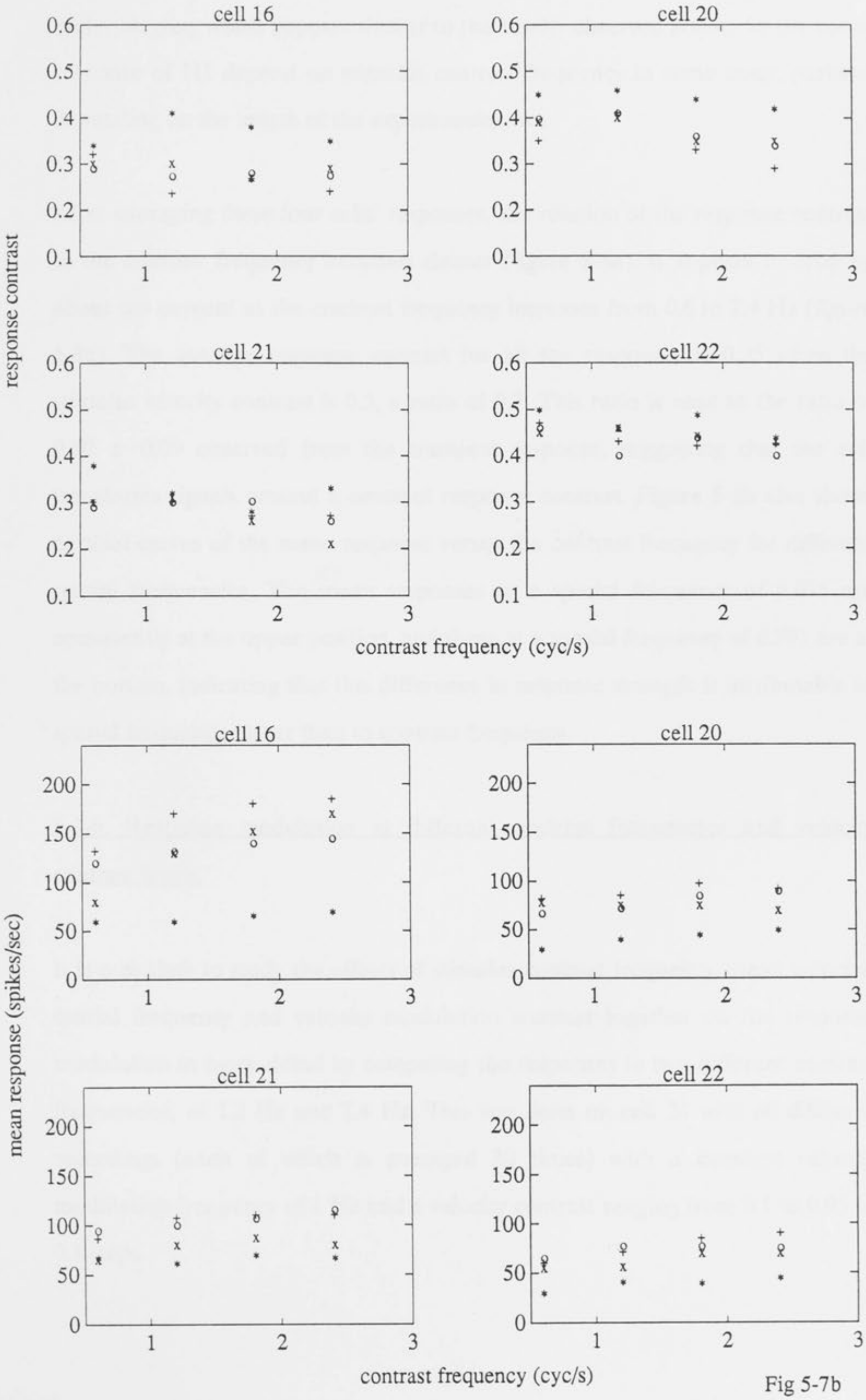

cell 16
cell 20
cell 21
cell 22
response contrast
contrast frequency (cyc/s)
mean response (spikes/sec)
contrast frequency (cyc/s)

Fig 5-7b

cycles/degree, and fall to the lowest level at a spatial frequency of 0.301 cycles/degree, which appears similar to the results observed above. So the mean response of H1 depend on stimulus contrast frequency in some cases, perhaps depending on the length of the experimental run.

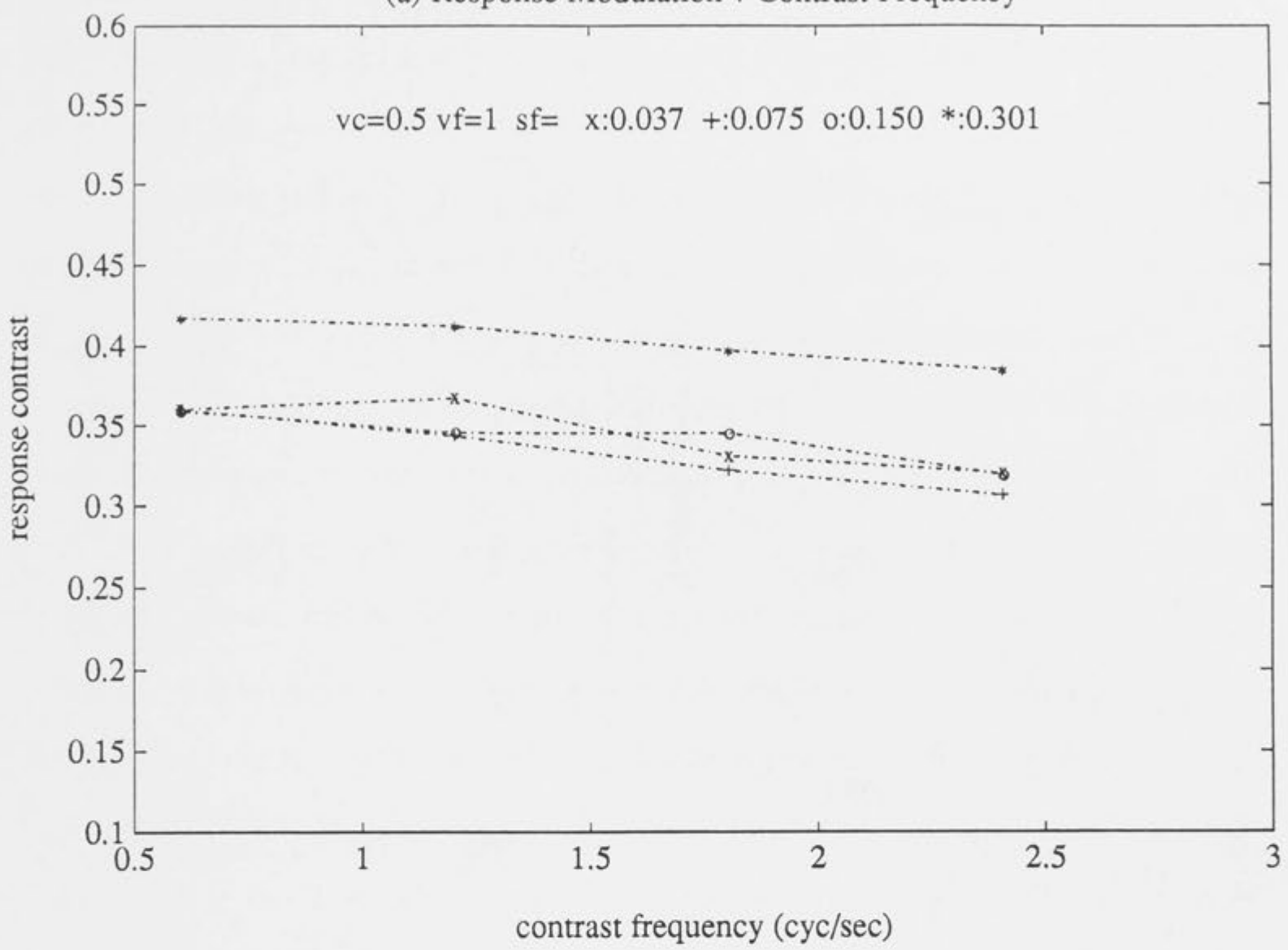
After averaging these four cells' responses, the relation of the response contrast to the contrast frequency becomes clearer (figure 5-8a). It appears to drop by about ten percent as the contrast frequency increases from 0.6 to 2.4 Hz (figure 5-8a). The average response contrast for all the responses is 0.35 when the stimulus velocity contrast is 0.5, a ratio of 0.7. This ratio is near to the ratio of 0.60 ± 0.09 observed from the transient response, suggesting that the cell transforms signals around a constant response contrast. Figure 5-8b also shows parallel curves of the mean response versus the contrast frequency for different spatial frequencies. The mean responses to a spatial frequency of 0.075 are consistently at the upper position, and those at a spatial frequency of 0.301 are at the bottom, indicating that this difference in response strength is attributable to spatial frequency rather than to contrast frequency.

5-3-6. Response modulation at different contrast frequencies and velocity contrast levels.

It is now time to study the effects of stimulus contrast frequency, mean velocity, spatial frequency and velocity modulation contrast together on the response modulation in more detail by comparing the responses to two different contrast frequencies, of 1.2 Hz and 2.4 Hz. This was done on cell 24 with 86 different recordings (each of which is averaged 30 times) with a constant velocity modulation frequency of 1 Hz and a velocity contrast ranging from 0.1 to 0.95 in 0.1 steps.

Figure 5-8. Average response contrast and mean response versus contrast frequency. The data were averaged from cell 16, cell 20, cell 21, and cell 22. The symbols of "x", "+", "o" and "*" represent either (a) the average response contrast or (b) the average mean response to stimulation at the spatial frequencies 0.037, 0.075, 0.15 and 0.3 cyc/deg, respectively. To keep a constant stimulus contrast frequency for four spatial frequencies, the mean velocity was correspondingly adjusted at four values. Looking at the figure, we see that the contrast frequency has very little influence on the response contrast. As the contrast frequency increased by 4 times, i.e. from 0.6 cyc/s to 2.4 cyc/s, the response contrast only decreased slightly by about 5%. As expected, to a constant contrast frequency, the cells produced four different strengths of responses to four combinations of the mean velocity and the spatial frequency. Normally, the cells had a stronger response contrast to a higher spatial frequency and a slower mean velocity. Secondly, the cells usually produced a bigger mean response to a lower spatial frequency and faster mean velocity, and slightly increased the mean responses as the contrast frequency increased. The large-field motion-detection neurons clearly do not measure contrast frequency.

(a) Response Modulation v Contrast Frequency



(b) Mean Response v Contrast Frequency

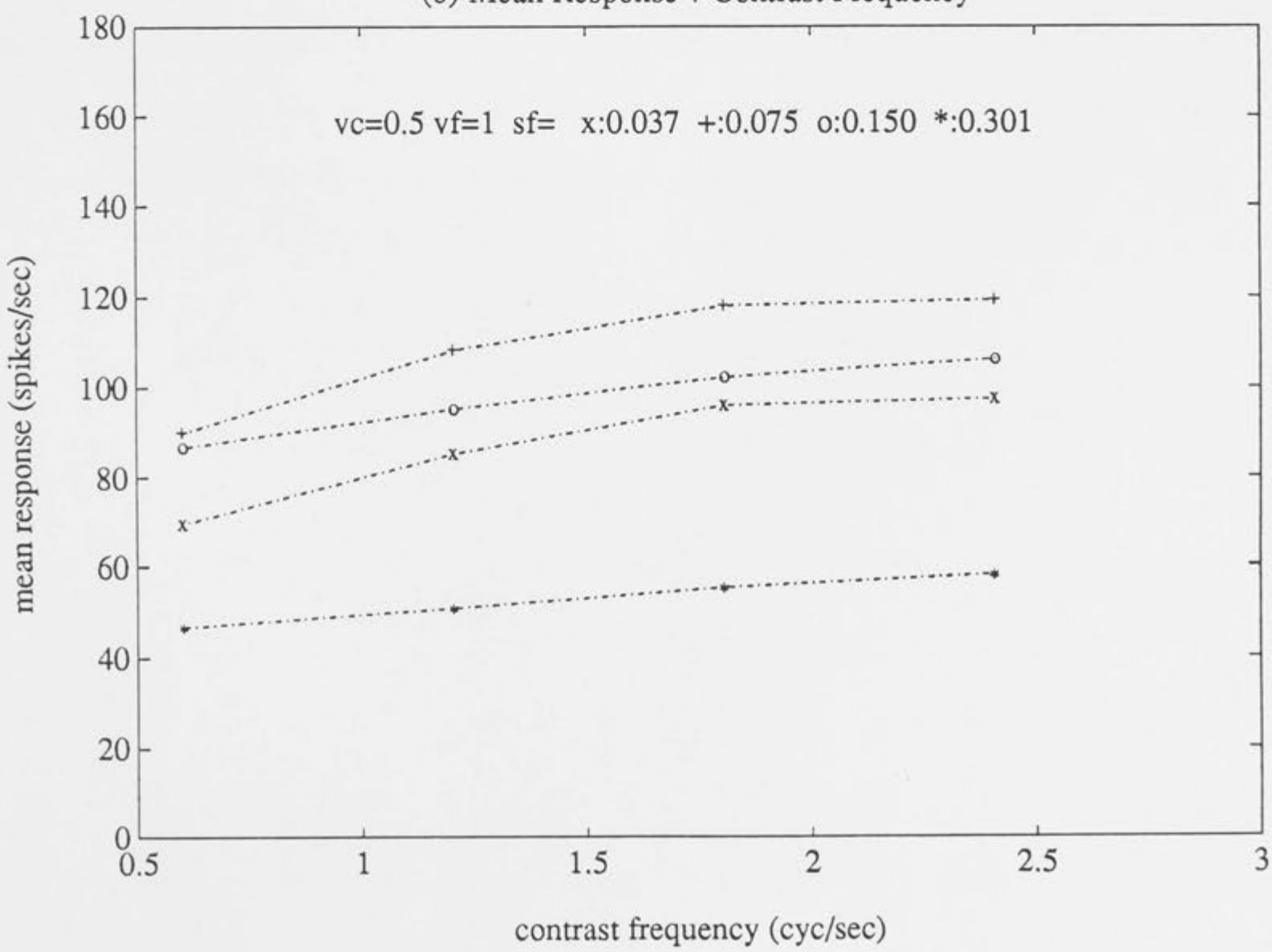
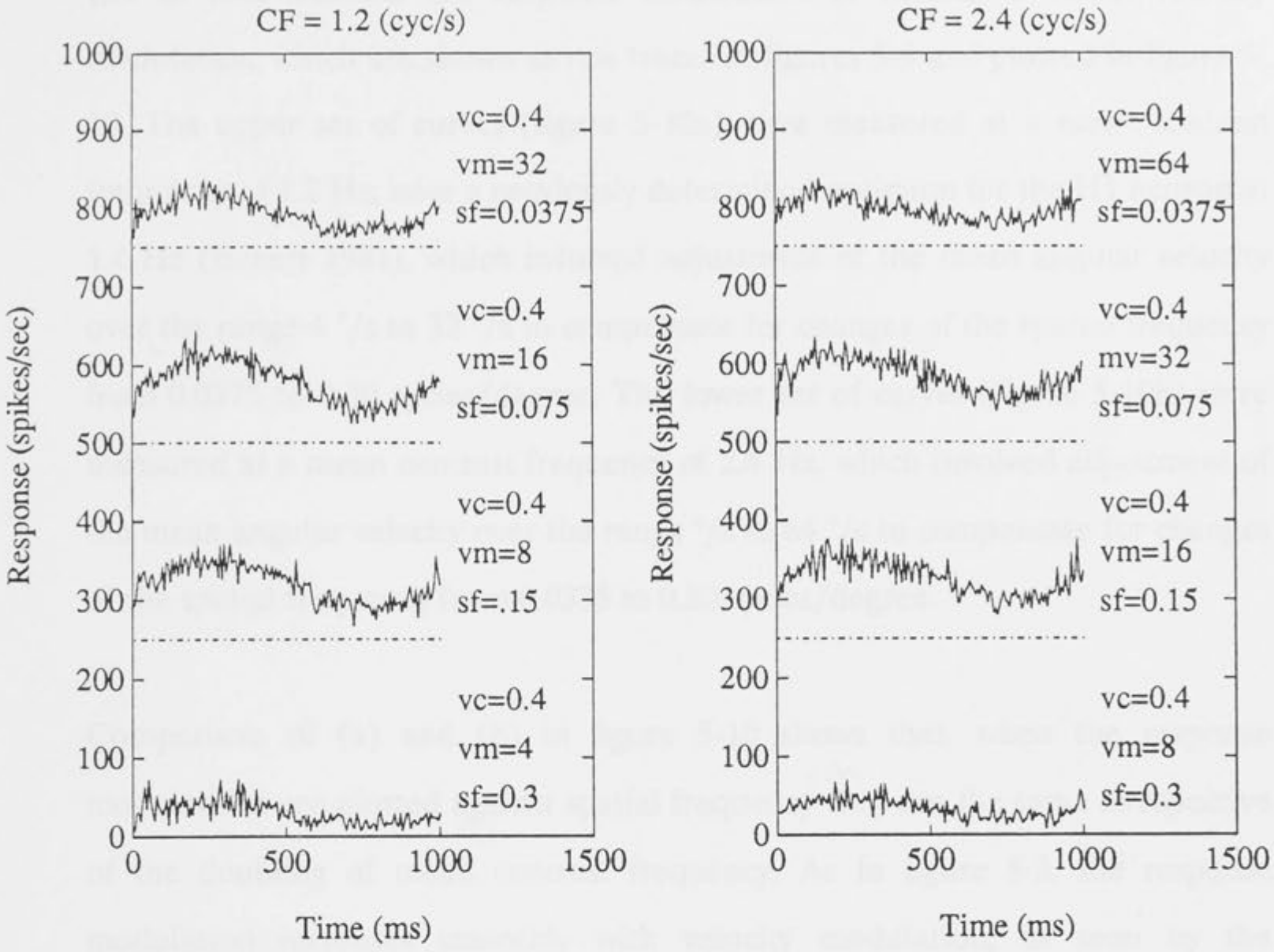
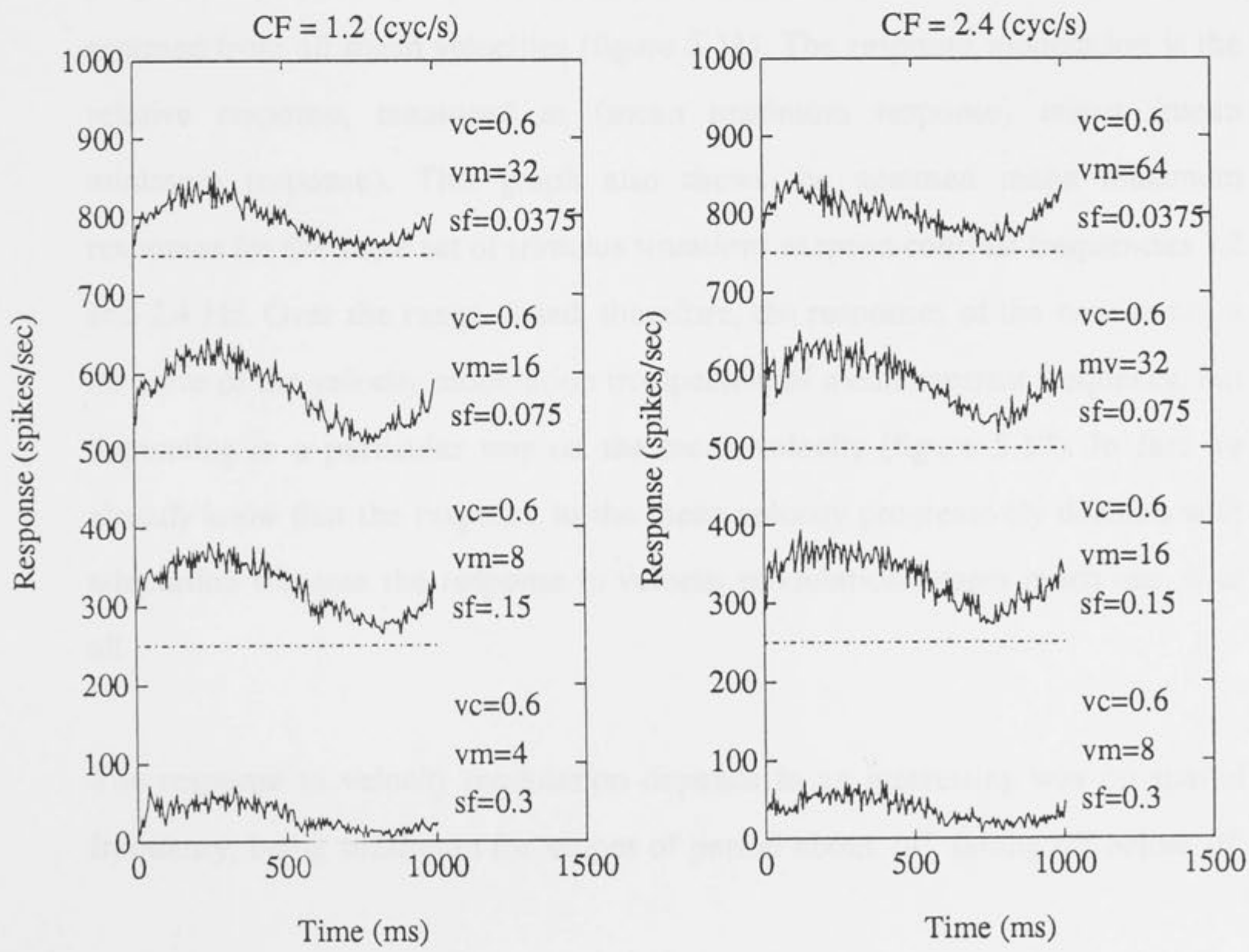


Figure 5-9. Records of response to velocity modulated stimuli. The vertical axis is the average spike frequency over 50 repetitions. The horizontal axis is phase-locked to the modulation of angular velocity of the stimulus, all at velocity modulation frequency 1 Hz. Therefore each record is one second long. The four horizontal rows are at four different spatial frequencies - 0.0375, 0.075, 0.15 and 0.3 cyc/deg, and at four different mean angular velocities over the range 4 °/s to 64 °/s to retain a constant contrast frequency 1.2 Hz (the left column) or 2.4 Hz (the right column). The upper sets have velocity modulation contrast 0.4, and the lower two have velocity contrast 0.6. This is some of the primary data plotted in figure 5-10. The dashdot lines are relative zero response base lines, CF presents stimulus contrast frequency, vc means velocity modulation contrast, vm means mean angular velocity (°/s), sf means stimulus spatial frequency (cycles/degree). Comparison of the responses in these four sub-figures demonstrates clearly that the responses are independent of the contrast frequency with very similar response strength and modulation to two contrast frequencies (see the left column and the right column), but with different strength and modulation to one contrast frequency (see responses in each of four sub-figures). There are different response strengths and modulations to different velocity contrasts (see the upper two sub-figures and the lower sub-figures). The stimulus spatial frequency is also a factor, with the biggest response to the spatial frequency 0.075 cyc/deg.


CF = 1.2 (cyc/s)
CF = 2.4 (cyc/s)
Response (spikes/sec)
Time (ms)
vc=0.4
vm=32
sf=0.0375
vc=0.4
vm=16
sf=0.075
vc=0.4
vm=8
sf=.15
vc=0.4
vm=4
sf=0.3
vc=0.4
vm=64
sf=0.0375
vc=0.4
mv=32
sf=0.075
vc=0.4
vm=16
sf=0.15
vc=0.4
vm=8
sf=0.3
0
100
200
300
400
500
600
700
800
900
1000
0
500
1000
1500

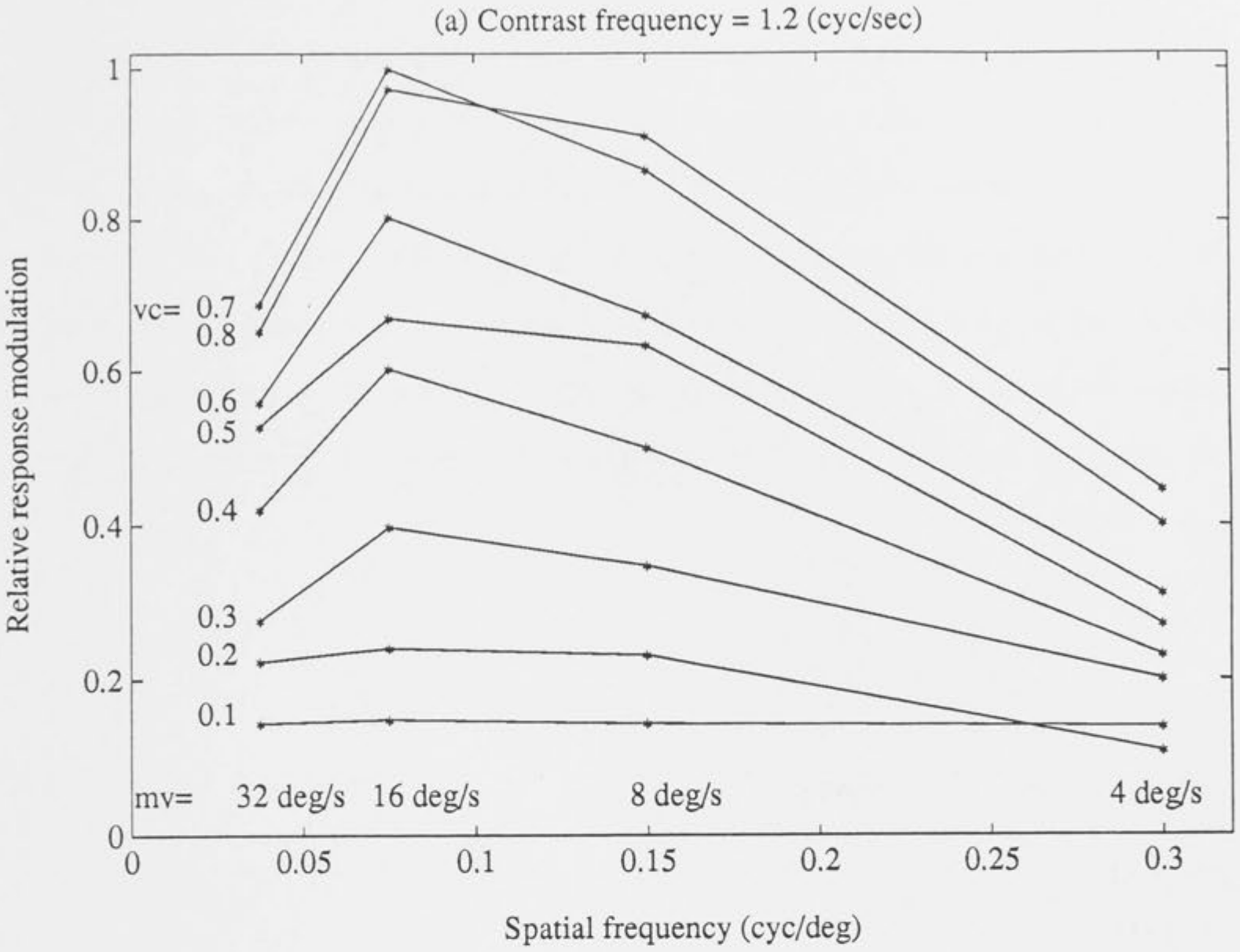

CF = 1.2 (cyc/s)
CF = 2.4 (cyc/s)
Response (spikes/sec)
Time (ms)
vc=0.6
vm=32
sf=0.0375
vc=0.6
vm=16
sf=0.075
vc=0.6
vm=8
sf=.15
vc=0.6
vm=4
sf=0.3
vc=0.6
vm=64
sf=0.0375
vc=0.6
mv=32
sf=0.075
vc=0.6
vm=16
sf=0.15
vc=0.6
vm=8
sf=0.3
0
100
200
300
400
500
600
700
800
900
1000
0
500
1000
1500

Let us first examine the response modulation to various levels of velocity modulation, which are shown as raw traces in figures 5-9 and plotted in figure 5-10. The upper set of curves (figure 5-10a) were measured at a mean contrast frequency of 1.2 Hz, near a previously determined optimum for the H1 neuron at 1.4 Hz (Eckert 1981), which involved adjustment of the mean angular velocity over the range 4 °/s to 32 °/s to compensate for changes of the spatial frequency from 0.0375 to 0.30 cycles/degree. The lower set of curves (figure 5-10b) were measured at a mean contrast frequency of 2.4 Hz, which involved adjustment of the mean angular velocity over the range °/s to 64 °/s to compensate for changes of the spatial frequency from 0.0375 to 0.30 cycles/degree.

Comparison of (a) and (b) in figure 5-10 shows that, when the response modulations are plotted against spatial frequency they are the same irrespective of the doubling of mean contrast frequency. As in figure 5-3, the response modulation increases smoothly with velocity modulation, as seen by the progressively higher peaks in figure 5-10, and as plotted from the same data summed from all mean velocities (figure 5-11). The response modulation is the relative response, measured as (mean maximum response) minus (mean minimum response). This graph also shows the summed mean maximum responses for the same set of stimulus situations at mean contrast frequencies 1.2 and 2.4 Hz. Over the range tested, therefore, the responses of the neuron are a measure of the velocity modulation irrespective of mean contrast frequency, but depending in a particular way on the mean velocity (figure 5-10). In fact we already know that the response to the mean velocity progressively declines with adaptation whereas the response to velocity modulation adapts much less, if at all.

The response to velocity modulation depends in an interesting way on spatial frequency, being maximum for stripes of period about 14°, falling off below 10°

Figure 5-10. The response modulation as a function of spatial frequency for a range of velocity modulations, at two contrast frequencies (a) 1.2 Hz and (b) 2.4 Hz. The four sets of measurements, made at spatial frequencies of 0.3, 0.15, 0.075 and 0.0375 cycles per degree, were done at mean velocities of 4 °/s, 8°/s, 16 °/s and 32 °/s in (a) and 8 °/s, 16 °/s, 32 °/s and 64 °/s in (b). The response modulation is measured as (mean maximum response) minus (mean minimum response). The value at the left side of each curve presents the stimulus velocity contrast used in this curve. The mean angular velocity at the bottom of each point is a velocity used for all the velocity contrasts over the range 0.1 to 0.8 at this column. This way of plotting the data shows that the response to velocity modulation is not changed by doubling the contrast frequency, but is affected by the stimulus spatial frequency. Also, it shows that the responses saturate for velocity contrast greater than 0.7.


(a) Contrast frequency = 1.2 (cyc/sec)
Relative response modulation
vc= 0.7
0.8
0.6
0.5
0.4
0.3
0.2
0.1
mv= 32 deg/s 16 deg/s 8 deg/s 4 deg/s
0
0.2
0.4
0.6
0.8
1
0 0.05 0.1 0.15 0.2 0.25 0.3
Spatial frequency (cyc/deg)

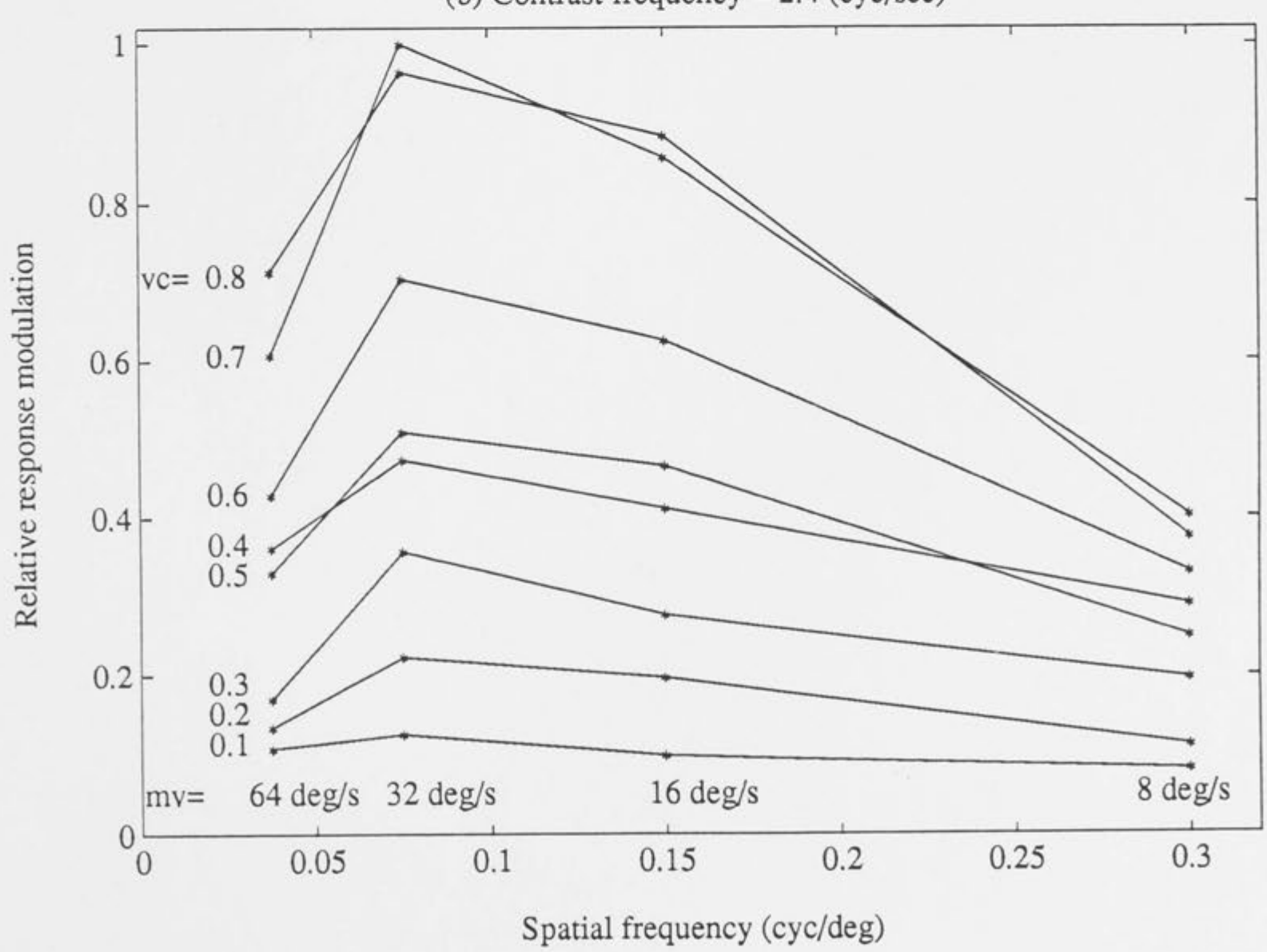
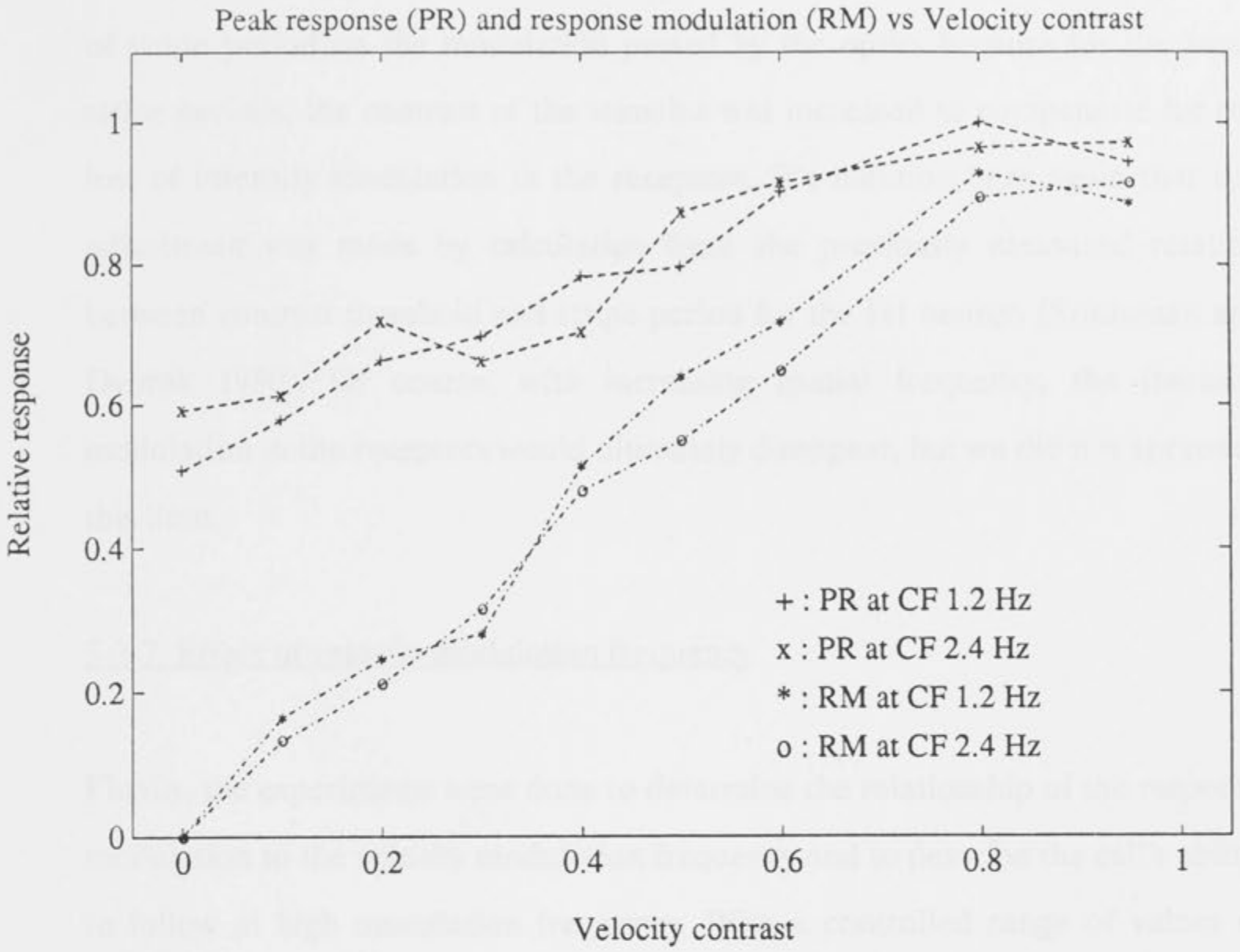

(b) Contrast frequency = 2.4 (cyc/sec)
Relative response modulation
vc= 0.8
0.7
0.6
0.4
0.5
0.3
0.2
0.1
mv= 64 deg/s 32 deg/s 16 deg/s 8 deg/s
0
0.2
0.4
0.6
0.8
1
0 0.05 0.1 0.15 0.2 0.25 0.3
Spatial frequency (cyc/deg)

Figure 5-11. The response as a function of the velocity contrast at two contrast frequencies, showing again linearity of peak response (PR) and response modulation (RM) on the stimulus velocity contrast, and saturation at about velocity contrast 0.8. The peak responses are partly attributable to the background velocity and therefore do not fall to zero. The values plotted here are the totals summed for the four different 4 °/s, 8 °/s, 16 °/s and 32 °/s. spatial frequencies, but it is apparent from the spacing of curves in figure 5-10 that similar curves would be obtained at each spatial frequency.


Peak response (PR) and response modulation (RM) vs Velocity contrast
Relative response
Velocity contrast
0
0.2
0.4
0.6
0.8
1
+ : PR at CF 1.2 Hz
x : PR at CF 2.4 Hz
* : RM at CF 1.2 Hz
o : RM at CF 2.4 Hz

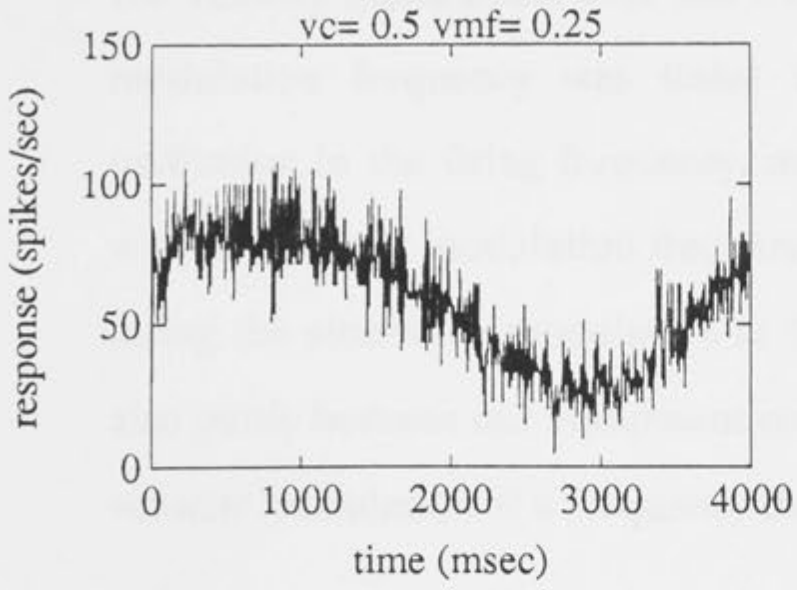
and above 20° (figure 5-10). These differences are not attributable to the effect of stripe period on the modulation passed by the optics because for the small stripe periods, the contrast of the stimulus was increased to compensate for the loss of intensity modulation in the receptors. We mention here again that this adjustment was made by calculation from the previously measured relation between contrast threshold and stripe period for the H1 neuron (Srinivasan and Dvorak 1980). Of course, with increasing spatial frequency, the intensity modulation in the receptors would ultimately disappear, but we did not approach this limit.

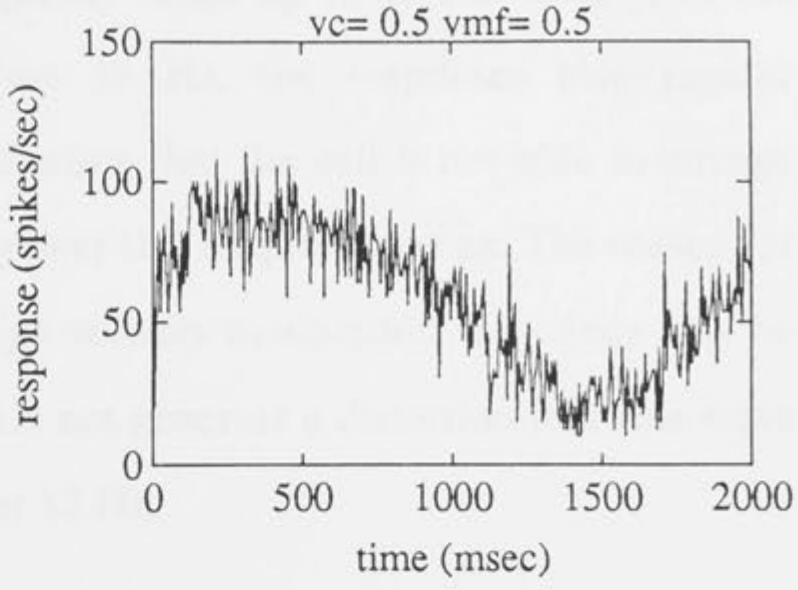
5-3-7. Effect of velocity modulation frequency

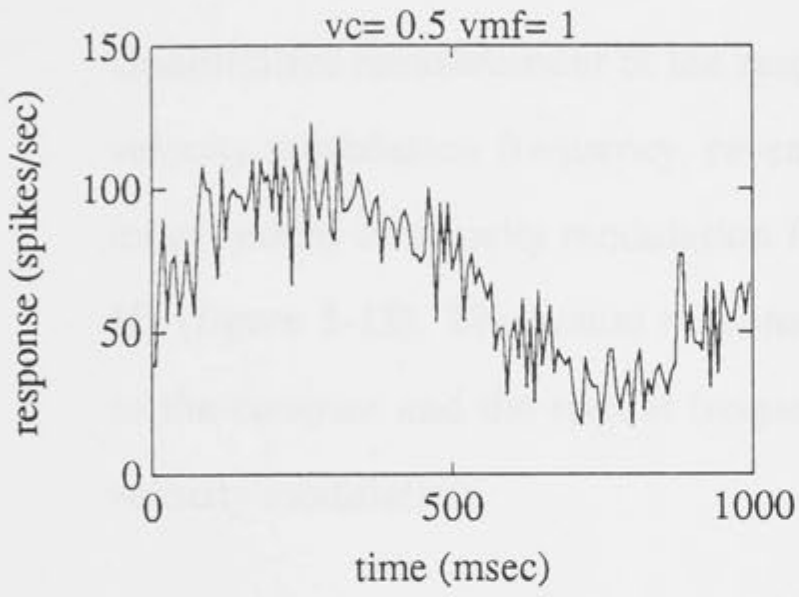
Finally, the experiments were done to determine the relationship of the response modulation to the velocity modulation frequency and to describe the cell's ability to follow at high modulation frequency. With a controlled range of values of mean velocity, spatial frequency, contrast frequency and velocity modulation, the velocity modulation frequency was changed over the range 0.25 to 32 Hz, the most that could be achieved with the equipment, and the responses measured as before as the modulation of the spike rate and also as the peak mean spike rate.

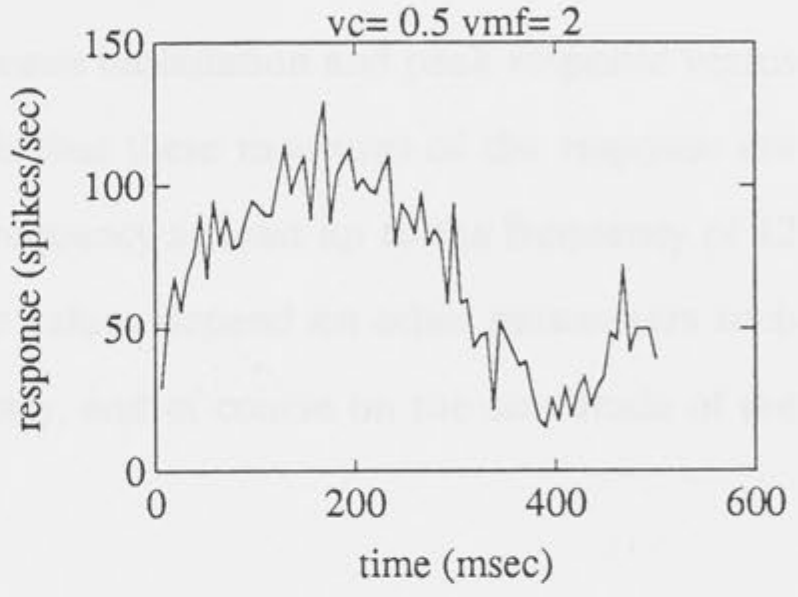
Examples of response modulation versus velocity modulation frequency at the mean velocity of 12 °/s and at the modulation contrast of 0.5 are plotted in figure 5-12, clearly showing that over the range from 0.25 Hz to 2 Hz, the responses of the cell are modulated in a perfectly sinusoidal way, which appears to be just a repetition of the velocity modulation, with a constant mean response at about 60 spikes/s and a constant response contrast of about 0.48. When the modulation frequency changes from 4 Hz to 12 Hz (which is not shown in the Fig.5-12), the sine-wave modulation seems to be progressively distorted but still oscillates in a regular way, which may be a indication that the cell is still capable of following

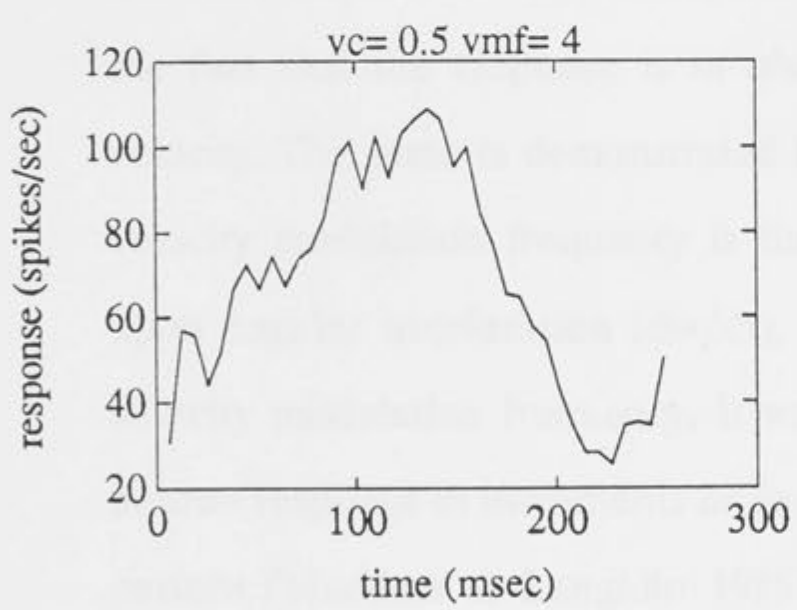
Figure 5-12. Demonstration that the H1 neuron follows velocity modulation over the frequency range from 0.25 Hz to 32 Hz. The stimulus pattern was a sine wave grating of spatial frequency 0.15 cyc/deg and intensity contrast 0.3, moving at mean velocity 12 °/s with velocity modulation contrast (vc) 0.5. The recording time at velocity modulation frequency (vmf) 0.25 Hz was 240 seconds; the time at 0.5 Hz was 120 seconds; the other records were 60 seconds, so the higher the frequency, the more the repetitions. The neuron can faithfully catch the modulation frequency over the range from 0.25 Hz to 2 Hz, showing a perfect sine-wave oscillation with constant response strength and modulation contrast. When the frequency increased to 8 Hz, the sine wave oscillation was gradually distorted but the response contrast shows that the neuron still follows the velocity modulation. Beyond 16 Hz, the response was more distorted but still present.

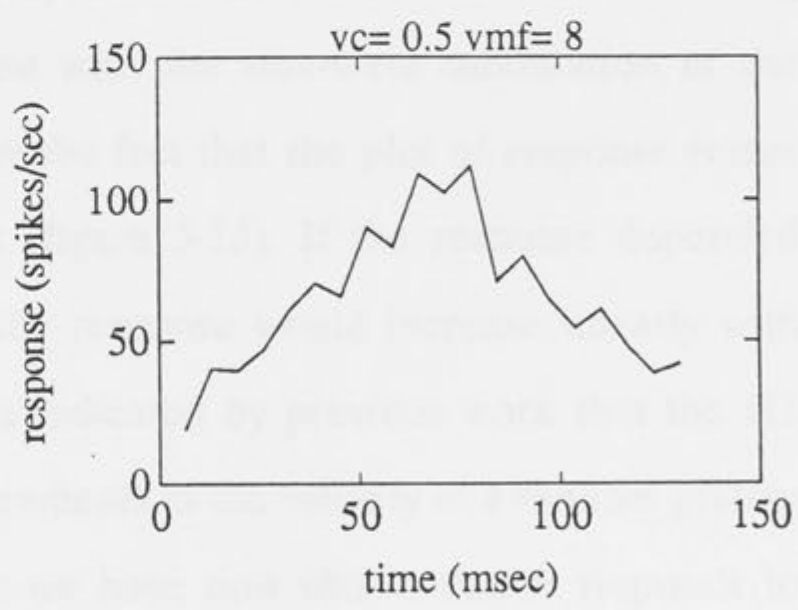

vc= 0.5 vmf= 0.25
response (spikes/sec)
time (msec)
0
50
100
150
0
1000
2000
3000
4000

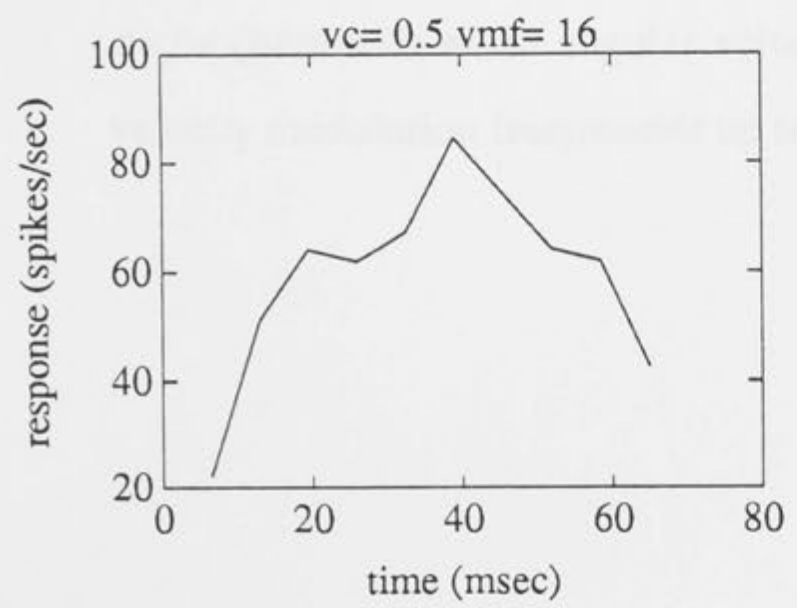

vc= 0.5 vmf= 0.5
response (spikes/sec)
time (msec)
0
50
100
150
0
500
1000
1500
2000

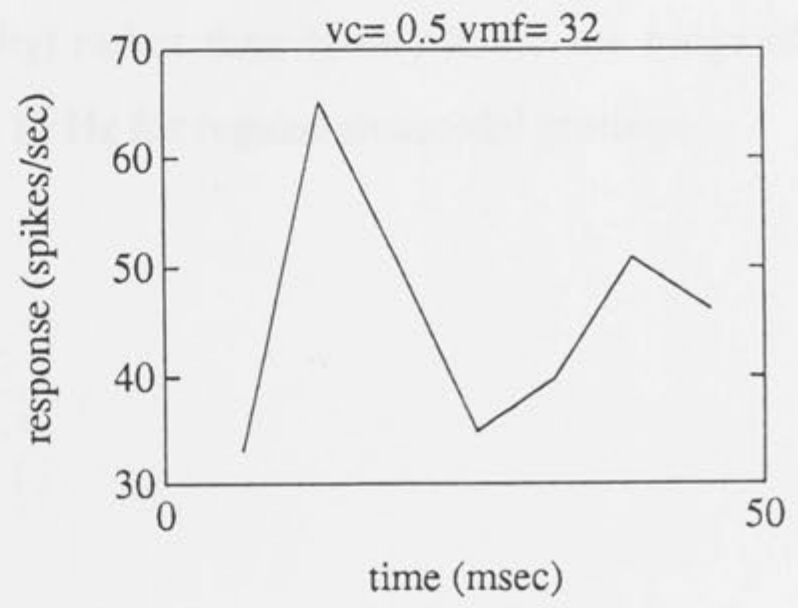

vc= 0.5 vmf= 1
response (spikes/sec)
time (msec)
0
50
100
150
0
500
1000


vc= 0.5 vmf= 2
response (spikes/sec)
time (msec)
0
50
100
150
0
200
400
600


vc= 0.5 vmf= 4
response (spikes/sec)
time (msec)
20
40
60
80
100
120
0
100
200
300


vc= 0.5 vmf= 8
response (spikes/sec)
time (msec)
0
50
100
150
0
50
100
150


vc= 0.5 vmf= 16
response (spikes/sec)
time (msec)
20
40
60
80
100
0
20
40
60
80

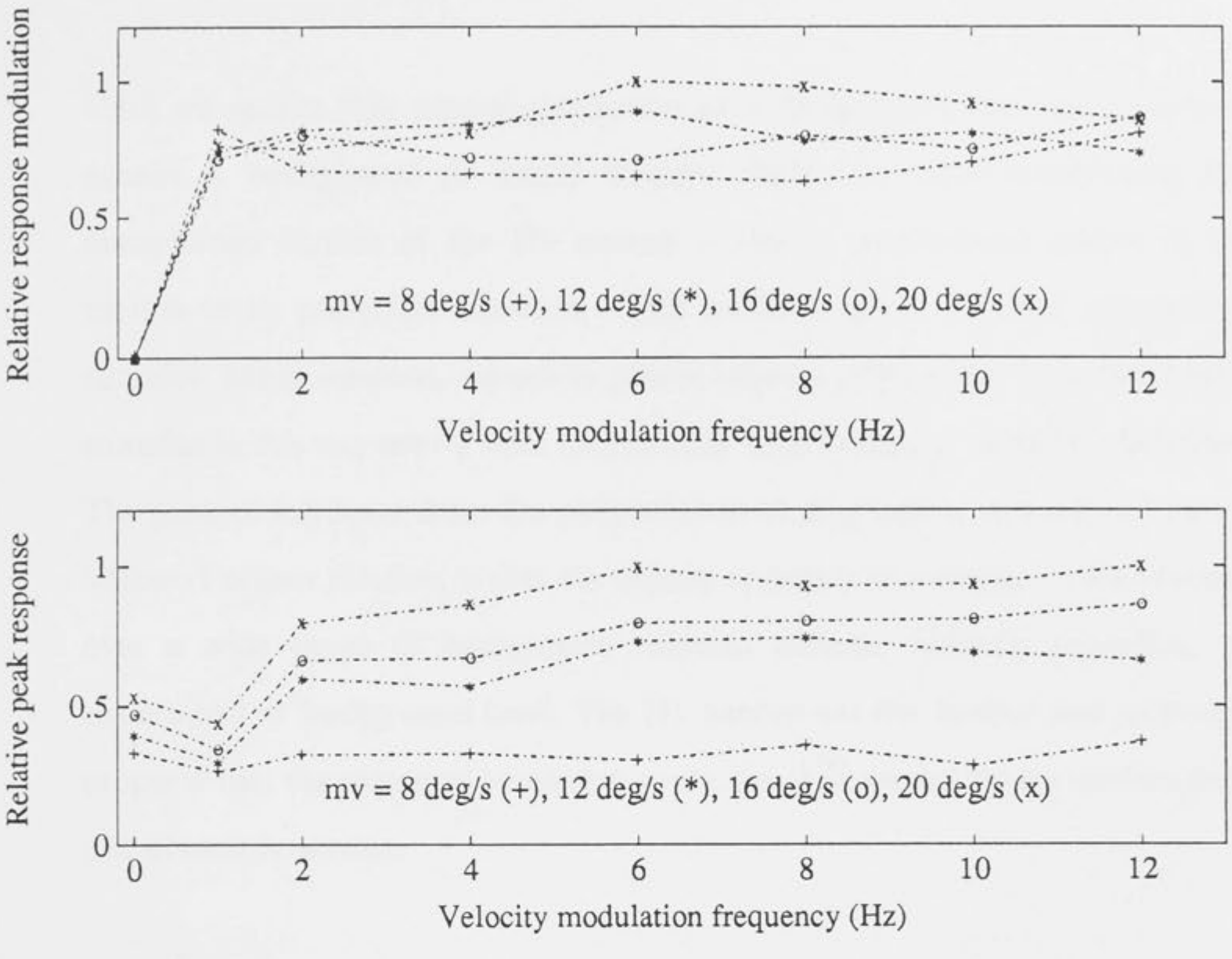

vc= 0.5 vmf= 32
response (spikes/sec)
time (msec)
30
40
50
60
70
0
50

the velocity modulation over the frequency range up to 12 Hz. Finally, as the modulation frequency was faster than 16 Hz, the responses lose regular oscillation in the firing frequency, indicating that the cell is not able to change with the velocity modulation frequency over this frequency range. The reason for losing the sine-wave modulation at high velocity modulation frequency may be also partly because our equipment could not generate a distortion-free sine-wave velocity modulation at a frequency over 12 Hz.

Quantitative measurement of the response modulation and peak response versus velocity modulation frequency, reveals that these measures of the response are independent of velocity modulation frequency at least up to the frequency of 12 Hz (figure 5-13). The actual response values depend on other parameters such as the contrast and the spatial frequency, and of course on the amplitude of the velocity modulation.

That the H1 neuron responds to velocity contrast, not acceleration, is shown by the fact that the response is in phase with the sine-wave modulation of the velocity. The same is demonstrated by the fact that the plot of response versus velocity modulation frequency is flat (figure 5-13). If the response depended upon angular acceleration (dw/dt), the response would increase linearly with velocity modulation frequency. It was indicated by previous work that the H1 neuron responds to increments or decrements in the velocity of a random grating pattern (Maddess & Laughlin 1985); we have now shown that it responds to dw/w (here w is mean angular velocity) rather than to dw/dt, for the range of velocity modulation frequencies up to 12 Hz for regular sinusoidal gratings.

Figure 5-13. Response as a function of velocity modulation frequency at a velocity modulation contrast of 0.5. (a) The response modulation at four different mean velocities - 8 °/s (+), 12 °/s (*), 16 °/s (o), and 20 °/s (x). (b) Peak response at the same four mean velocities. The data were obtained from cell 24, with the same stimulus conditions as in figure 5-12. Plotting in this way demonstrates again that the response is independent of the velocity modulation frequency up to 12 Hz.


Relative response modulation
1
0.5
0
0
2
4
6
8
10
12
mv = 8 deg/s (+), 12 deg/s (*), 16 deg/s (o), 20 deg/s (x)
Velocity modulation frequency (Hz)

Relative peak response
1
0.5
0
0
2
4
6
8
10
12
mv = 8 deg/s (+), 12 deg/s (*), 16 deg/s (o), 20 deg/s (x)
Velocity modulation frequency (Hz)

5-4. DISCUSSION AND CONCLUSION

Until we realize that motion perception of a flying insect must be performed aganist a background of steady forward flight, the most outstanding and unexplained feature of the H1 neuron is that it continuously adapts to the motion in its preferred direction, which at first sight is its most appropriate stimulus. Many neurons, especially phasic sensory cells, adapt to a maintained stimulus in this way over a wide (but usually fixed) range of rates of adaptation. The general inference from the phenomenon of adaptation, summarized by the Weber/Fechner relation, is that the neuron responds to a change in the stimulus over a wide range of background stimulus without faithfully recording the maintained or background level. The H1 neuron has the further and surprising property that the temporal resolution to do this is improved by the motion itself just when it is needed.

5-4-1. Velocity contrast is equivalent to contrast frequency contrast

For a regular pattern, of spatial frequency (f) and angular velocity (w):

Contrast frequency = angular velocity * spatial frequency = w*f ... equ. (1).

Contrast frequency contrast = (w1*f1 - w2*f2)/(w1*f1+w2*f2) ... equ. (2).

So, if f is constant, f1=f2, then

equ. (2) = (w1 - w2)/(w1 + w2), so

contrast frequency contrast = velocity contrast equ. (3).

The velocity contrast describes the motion of the stimulus: the contrast frequency contrast describes the resulting temporal modulation of the flicker at each receptor. For constant spatial frequency, the velocity contrast is identical to the contrast frequency contrast. Therefore the unit motion detectors could

measure the directional contrast frequency contrast, irrespective of mean contrast frequency.

5-4-2. The action of the H1 neuron

We confirm by a different method the conclusion of Maddess and Laughlin (1985) that the H1 neuron, and by implication other large lobula plate neurons such as V2 that behave similarly, detect changes in velocity of a moving pattern and give a measure of their amplitude. The early work was restricted to an indication that sensitivity to increments and decrements of velocity increased with adaptation, that the response to a change in velocity is optimum around the adapting velocity and that the response to a constant velocity contrast is fairly independent of the adapting velocity. We have shown that responses increase with velocity modulation independently of background velocity, contrast frequency or velocity modulation frequency. We also found that at low intensity contrast the response to sinusoidal modulation of the velocity was also sinusoidal and in phase, at least up to 12 Hz. Therefore the response is to velocity modulation, not acceleration, and the background velocity is not of great interest to this neuron. Indeed, we can repeat that adaptation of H1 has the same effect on the response to motion as adaptation of the receptors has upon their response to light. Further, the adaptation is apparently a property of the unit motion detectors or directional templates because it is localized to the visual axes that are stimulated, and not influenced by the actual spike rate of the H1 neuron. Therefore, by analogy with the photoreceptors, which report changes in photon flux, the unit motion detectors report changes in motion and the response of the directional motion templates, whatever they are, follow the Weber-Fechner relationship, like photoreceptors.

5-4-3. The mechanisms involved

Electrophysiology has not yet uncovered the unit motion detectors, which have so far only been inferred from the spatial resolution of large field motion detection. Three different ideas about the mechanism have been aired. All agree with the observation that the steady state response is independent of the pattern when plotted against the contrast frequency, but this is true for any mechanism which gives a unit response to the passing of each edge, especially when the effect of increasing contrast saturates at a low contrast level. The autocorrelation theory of Reichardt (1961) is the most popular. It is a steady state theory which has been extended to account for adaptation (Egelhaaf & Borst 1989). Essentially it is a way of mainipulating the stimulus pattern to predict a single final output. By choice of parameters, the output is fitted to the input, with no assistance to those seeking neural mechanisms. The second idea is that pairs of neuron terminals from adjacent visual axes make an asymmetrical compound synapse upon a dentrite of the motion detector neuron with sufficient time constants to fit to the required output. These are minimal theories, the simplest to fit the results, and not mutually exclusive. A third theory is that there is a group of templates which are repeated on each visual axis at the level of the medulla, and that these templates respond to combinations of contrast states at adjacent pairs of visual axes at successive times (Horridge 1990). The templates could be neurons or parts of neurons. Their essential feature is that they respond phasically as their own preferred features pass over them in the moving image, and the responses of the various templates are separatedly line-labelled so that they can be counted, or ratios taken, in the same way as different photoreceptor responses lead to colour vision. This is a very general theory that accounts for much more that the optomotor response. We can add that adaptation must also be a significant property of the unit motion detectors or templates.

5-4-4. What use is velocity contrast?

In the natural situation, with the moving animal in flight, there is a one-dimentional flow field expected at each point on the eye (except looking directly ahead). There are long-term mechanisms, such as overhead light acting via the compound eyes which keep the fly on an even keel (Hengstenberg 1989). Similar ocellar mechanisms have this function in some other insects (Wilson 1978). The most obvious features of the large-field motion-detection neurons are that they are phasic, high spatiotemporal resolution, very high gain, short-latency and directional, all of which can be accommodated by the template model. Errors in flight control must be corrected with the stiffest possible feed-back loop at maximum gain in the right direction. The urgent requirement is the qualitative sign of the response and it may be incidental that anything is measured quantitatively. The relation between velocity contrast and response modulation may simply be an arbitrary consequence of having many templates in parallel all adapting to background motion but optimizing their ability to give an immediate response to a transient in the preferred direction.

CHAPTER SIX

GENERAL DISCUSSION

The large field motion detectors, especially the H1 and V2 neurons, turned out to be an apparently simple but in fact very one-sided model system for the study of how signals are processed (Reichardt and Poggio 1976; Poggio and Reichardt 1976; Srinivasan and Dvorak 1980; Buchner 1984; Reichardt 1986; Horridge 1990). The principles of motion detection tested on the H1 neuron have been extended to explain motion detection in other species, even man (van Doorn and Koenderink 1982a, b; van Santen and Sperling 1984; Baker and Braddick 1985; Wilson 1985), but, in fact, only with respect to a very limited aspect of motion perception. Briefly speaking, the motion signals, in the first step of their evaluation, are captured locally by some local input units, called EMD's (elementary motion detectors) or bilocal detectors, each of which is assumed to be an interaction of two neighbouring retinal input channels in both time and space as originally proposed by Hassenstein & Reichardt (1956), funneling into neurons, called large field motion detectors, apparently related to optomotor functions. However, whether the horizontal and vertical neurons share the same or similar input channels, whether there is only one kind of motion channel in transforming the motion signals from the EMDs to the LFMDs or not, and what they measure, are further studied in our experiments.

6-1. The similarity of the H1 and V2 neurons.

A motion in any direction in the two-dimensional image on the eye can be resolved into two vectors - horizontal and vertical. Perhaps not coincidentally, the large field motion-sensitive neurons of the lobula plate also fall into two

groups - the horizontal and the vertical motion-detectors (Hausen 1981; Hengstenberg 1982). Theoretically, these two groups of neurons on the two sides are together capable of detecting any motion - rotatory (yaw, roll, pitch) and translatory (lift, thrust, side-slip) movements, so it is natural to test whether they have the same or similar properties in processing motion information. Supposing that the large-field motion-detection has three stages - first the input properties, then the motion processing mechanism and finally the impulse initiation stage, the above results demonstrate a strong similarity between H1 and V2 neurons in all three stages.

6-1-1. Physiological similarity of H1 and V2.

Comparing the responses of H1 and V2 to the stimulus of a moving grating or a bar, it is found that they have very similar physiological characteristics, in the following ways. Both have a similar size of receptive field covering the major part of the opposite eye, revealing that both receive visual inputs distributed from similar regions of the eyes. They respond to movement of similar time course with transient and steady state stages, and with similar increment and decrement time constants which probably reflect similar low and high pass filters in signal transformation. Also the response speed of both cells reveals no difference in the latency and time to peak (Fig.4-9), indicating that both types of cells may process the signals by similar circuits and via the same number of synapses. Their firing frequency is over a range from 20 spikes/s to 400 spikes/s, though H1 is more active than V2. To varied jump angles of a bar, both of them have the same shape of the response-displacement curves (Fig.4-7, Fig.4-9 and Fig.4-10), with the stimulus threshold at about 0.1°. And both have similar velocity discrimination capable of encoding the velocity linearly to 56 °/s in the transient response and to 40 °/s in the steady state (Fig.4-7). They possess the same triangle-shaped curves with 2.2° width at two thirds of the peak when the

transient response is plotted against stimulus displacement (Fig.4-9a & 4-10). This field apparently reflects the spatial spread of the individual EMD's with optimum width 2.2°, because the spatial sampling pattern involved in the motion detection is based on a spread of 2 or 3 interommatidia (Tinbergen 1987; Schuling et al, 1989). The transient response strengths of both are linearly dependent on the displacement in a range from 0.1° to 0.65° during the integration time (Fig.4-4), which decreases from 40 ms to 6.5 ms with increase of stimulus speed from 16 °/s to 80 °/s (Fig.15 shows a result from H1), exhibiting a capability of measuring the stimulus displacement linearly up to 0.65°.

After seeing a stationary periodical pattern, the response of H1 and V2 to movement of the pattern exhibits an interesting feature - the afterimage (Fig.3-1) - so that the amplitude of the response oscillates at the temporal frequency of the stimulation (Fig.3-2). During the afterimage V2 temporarily loses its directional selectivity (Fig.3-4), in agreement with the previous finding on the H1 neuron (Maddess, 1986). For both neurons, the afterimage can be eliminated by a prior motion, even at a very slow speed of 8 °/s (Fig.3-3), indicating that both cells rebuild their directional selectivity after responding to a movement for 2 seconds. The afterimage apparently indicates some intrinsic properties of the unit motion detectors. The short term memory may lie in the EMD's during the transient state (Maddess, 1986); or there is a low pass filter before the movement-detection interaction of the visual inputs (Egelhaaf, 1988). The responses of H1 and V2 to the jump of a bar are also both influenced in the same way by a prior-motion, exhibiting a strong negative phase following the first peak (Fig.4-12).

6-1-2. Morphological similarity of H1 and V2.

The similarity of the response properties is probably correlated with the similarity of the location of the dendrites of these two neurons in the lobula plate. Among those tangential cells of the lobula plate of the fly so far marked and recorded, only H1 and V2 are heterolateral whole-field neurons connecting both lobula plates, with large dendritic domains in both sides (Hausen 1976a, b & c; Hausen & Egelhaaf 1989; Eckert 1980 & 1982; Hengstenberg 1982; Strausfeld 1984). Although there is no direct proof of H1 and V2 assembling and sending signals by similar nervous circuits, the anatomical and physiological evidences found so far do support that idea (Bishop et al. 1966, 1981; Marmarelis & McCann 1973; Hausen 1976).

6-1-3. The similarity in the inputs level of H1 and V2.

The similarity in the responses of the H1 and V2 neurons must be referred to the processing elements, especially the elementary motion detectors - the presumed basic functional units in the first step of the processing motion signals. According to this assumption, all of the transient response of the LFMDs represents the properties of EMDs (Egelhaaf & Borst 1989; van Hateren 1990), and it is now proposed that H1 and V2 may share EMDs with similar temporal and spatial properties. The results are in full agreement with Srinivasan's proposition (1983) based on H1 that the EMDs measure the stimulus displacement during the transient response, and may support the template model in that EMDs simply respond to passing edges (Sobey & Horridge 1990). Also, the transient response duration of H1 and V2 remains constant, which means that they cannot discriminate the length of stimulation during that period. The integration time apparently becomes a measure of the EMD's temporal resolution, which is improved by a faster stimulus for both neurons.

The EMDs - whatever they are - play a fundamental role in determining the ultimate properties of the LFMDs. If H1 and V2 collect the motion signals from similar EMDs, as suggested, the final response characteristics must be similar. In fact, there are some alternative ways of using similar EMDs as inputs for both H1 and V2 neurons. One way is to consider the inputs of H1 and V2 as just the horizontal and vertical components of the EMD's responses (Buchner 1976; Franceschini 1975 & 1985; van Hateren 1987 & 1990). A single EMD then consists of four basic motion detectors, a positive and negative ON-EMD and OFF-EMD, which are derived from two neighbouring retinula cells in the same ommatidium, for example from R1 to R6 (Franceschini et al. 1989; Kirschfeld 1972). So, within one ommatidium, six functionally similar EMDs can be formed with preferences in six different directions across the retina, the basic horizontal motion detection is just the sum of horizontal components, and the basic vertical motion detection normally needs the EMDs whose orientations are separated by 60° (van Hateren, 1990).

Of course, it is not necessary to assume only one kind of EMDs acting at the input level; and in fact it is not known whether, in morphological terms, there are separate EMDs in the visual pathways of the fly at all, although small-field motion detectors have been recorded in the medulla of the fly (DeVoe & Ockleford 1976; DeVoe 1980) and of the locust (Osorio 1987). Actually, any homogeneous network, whose elements interact positively or negatively laterally in one direction, can effectively detect movement in the preferred direction. Van Hateren showed that the measurement were compatible with the idea that the response of H1 is just a weighted non-linear sum of a group of the EMDs with different sampling distances of spatial interaction, but didn't demonstrate this (van Hateren 1990). We also know from tests done by Kirschfeld (1972) that there are certain directions of interactions between retinula cells on different but adjacent axes. Some of these may be sent separately to different giant cells of the

lobula plate, but, in general, the response properties of all of the motion detection neurons are similar.

By using sequential micro-stimulation of adjacent neuro-ommatidia of the blowfly compound eye, it was found that the spatial sampling pattern underlying visual movement detection is dominated by nearest-neighbour interactions between pairs of cartridges (EMD's), but sampling bases or lateral interactions also exist at 2, 4 and 6 times the interommatidial angle (Schuling et al, 1989). Similarly, experiments on fly landing behaviour indicated that the movement response can be elicited by simply stimulating those motion detectors whose spatial sampling bases are between 2 and 3 times the interommatidial angle (Tinbergen, 1987). The lateral interaction of neuro-ommatidia can take place even in a extended range to satisfy the task of detecting movement ranging from 0 to infinity (van Hateren, 1989). These results demonstrate the flexibility of lateral interactions in range and strength between the EMDs to form different kinds of motion channels in the LFMDs responses to object movements with or without prior-motion.

Summing up, the H1 and V2 neurons are similar in their responses to movements; due to processing motion signals in similar ways with similar inputs.

6-2. Two kinds of directional motion detection channels.

6-2-1. Theory and present results.

Fly directional motion detection has been widely studied in past decades. Any movement is first detected locally by distributed EMDs in parallel, with the spatial resolution of the retina, and their responses are assembled by large-field motion-detectors at the lobula plate for optomotor responses (Reichardt and Poggio 1979, Srinivasan & Dvorak 1980, Hausen 1983). However, some questions remain still open. Do all motion detection channels have similar temporal and spatial properties? Are all kinds of motion signals transferred into the LFMDs within the same pathways or are there other destinations beside the LFMD's? In this section it is proposed that the fly's motion detection system has two kinds of distinct motion channels. One set are band-pass or high-frequency channels, primarily detecting sudden movements, the other is more responsive to continued movements. It is assumed that the fly's motion detection system classifies moving objects into sudden or continued movements, and employs separate mechanisms to deal with each kind of movement.

This proposition is supported by the following results. The H1 and V2 neurons possess two kinds of response-velocity curves in response to brief jumps of a black bar. With prior-motion, the cells produce sigmoidal-shaped transient response curves (Fig.4-9 & 4-10); but without prior-motion, bell-shaped transient response curves appear (Fig.4-16). This significant difference is generated by the processing system itself. A hypothesis for this phenomenon is that the fly's motion detection system has two separate channels. The channels with sigmoidal-shaped response-curves are more suitable for the task of measuring velocity than the channels with bell-shaped curves. The sigmoidal-shaped response-curves will never confuse two speeds by producing the same strength of

response to two different speeds, but the channels with bell-shaped curves certainly will make this mistake. So the channels with sigmoidal-shaped response curves can participate in range-measurement or the control of landing. In contrast, the channels with bell-shaped curves are definitely not suitable for this kind of work for they indicate with accuracy only the direction of a movement.

So far, we do not yet know precisely where, along the visual pathway, these two kinds of motion detection channels may lie, if they are separate. Motion detection certainly does not take place in the retina, and happens before summing the EMD's in the lobula plate. Experiments with the activity-specific method with deoxyglucose suggest that the motion detectors may be in the medulla (Buchner et al., 1979). Direction-selective units have certainly been found in the medulla (DeVoe & Ockleford 1976; Osorio 1987). Now, let us provide some experimental support for our hypothesis that motion signals are transformed by two kinds of motion detection channels.

6-2-2. The new experimental evidence.

Firstly, the two kinds of motion detection channels may be formed at the level of the EMDs, which appear to have the ability to change their spatial and temporal parameters according to the stimulus. This idea actually has already been talked about for decades. In the early works of Buchner (1976) on the walking fly, the results suggest that the motion responses of the animal are dependent on a weighted sum of the outputs of different kinds of EMD's whose spatial interaction distances vary from the adjacent visual input elements to ones several visual axes away. The concept has been developed by van Hateren (1990), who points out that the spatial interaction between visual input elements can take place in various ranges to form EMDs with different spatial resolutions. Another model based on this idea is proposed by Srinivasan & Dvorak (1980), which

shows several types of EMDs with various ranges of spatial integrations at different levels of ambient light. Further results from the experiments on the H1 neurons, by using sequential micro-stimulation of two (or more) adjacent neuro-ommatidia in the compound eye of the blowfly, are also in agreement with these models (Schuling et al. 1989). The above arguments demonstrate the existence of more than one kind of EMD in the spatial domain, but only hint at EMDs with different temporal parameters. In fact, the EMDs with various spatial sampling ranges must also have different temporal measures. The EMDs composed of neighbouring ommatidia may be most sensitive to small movements or lower velocities. In contrast, the EMDs with long interaction ranges may be able to respond to greater velocities. From an experiment on visually guided orientation behaviour, Pick (1976) concludes that fly visual input elements that respond to flickering stripes contain two different mechanisms - a local flicker-detecting mechanism whose sampling ranges are limited to 3 vertical rows of ommatidia, and a specific directional interaction which is mediated by a field of interconnections of receptors separated by at least 4 to 6 vertical rows of ommatidia. In fact, the local flicker-detecting mechanism is very similar to the high-frequency channel, and the type with wider spatial separation is working in a similar way to our second kind of motion channel, so that both together can measure a wide range of speeds.

Unfortunately, there is not much direct evidence about different types of motion filters in fly EMDs. In fact, every effort has been made to explain fly motion perception in terms of a single channel. In general, all neurons can be divided into two groups in terms of their physiological properties - high pass or phasic and low pass or tonic neurons. This apparently applies to two kinds of specific motion detection filters with different movement preferences. The first is a band-pass filter with a bellshaped response versus velocity profile, with high pass in a certain range of velocity. Probably, these filters can be used only to catch a

sudden movement, especially from steady state motion and possibly only suitable for detecting motion direction and direction of velocity change within this velocity range. The other kind of motion filter would be a high-pass filter with a sigmoidal-shaped response curve but with a relatively low response gain, generally used for continued movement, and sensitive to a wide range of velocities. The response of the LFMDs is then a weighted sum of these filters, with final behaviour determined by which one dominates. With a background motion, the high-pass filters are favoured, and the temporal resolution is shortened, but with no motion the weighting is changed so that the band-pass channels determine the characteristics of the response. It is also known that the LFMDs are less acute in low light levels (Srinivasan & Dvorak 1980).

The idea of two channels is also supported by previous findings on the medulla of the fly (DeVoe 1976, 1980). Cells of the lamina chiasma and medulla can be roughly classified into sustaining cells and flicker ON/OFF cells in response to movement, and the responses included tonic and phasic components (Arnett 1972). Also the recent results with intracellular recording and marking in locust medulla (Osorio, 1986, 1987 & 1988) indicate the same classes. The medulla of the locust contains many non-directional small-field motion detectors with different temporal constants, some transient cells and others sustaining cells.

Other recent results on fly behaviour support the hypothesis of different channels for different motion signals. First, in the fly's yaw torque response, the compensatory optomotor turning reaction and the orientation response towards objects must be mediated separately by two kinds of parallel circuits (Reichardt 1979, 1986; Egelhaaf 1985 a-c, 1987 & 1989; Hausen & Wehrhahn 1990). Perception of global movements causing low oscillation frequencies of the yaw torque are controlled by the large-field motion-detection cells of the lobula plate (Hausen, 1982a, b). Local movements and high frequencies of yaw torque are

mainly detected by other, so-called FD cells forming the small-field motion-detection system (Egelhaaf 1985b, c). These two channels are proposed to act together in discriminating a target from its background (Egelhaaf 1987). About ten years ago, experiments on the tethered fly already suggested a similar model to predict how the fly discriminates local moving targets from the background movement (Reichardt & Poggio 1979). The above conclusions are not directly related to two kinds of EMDs, but suggest that the EMDs feed into two channels.

There is a fundamental problem as to how any visual system has available the right kind of channels to deal with expected signals. For motion there seems to be two kinds of transient responses selected by the prior motion state.

6-2-3. Short-term memory.

A fly can learn quickly an object movement and remember it for short periods (Geiger 1975). There is also good evidence of memory with regard to visual parameters, such as orientation, in the insect's nervous systems, especially in the honey bee (van Hateren, Srinivasan & Wait; 1990). Furthermore, experiments on bee visual behaviour suggest a probable pictorial memory in learning and remembering spatial patterns (Gould, 1985, 1986 and 1987). Four memory stages have been proposed - a working memory, an early memory, a late memory and a permanent memory (Menzel, 1978, 1983 and 1985). Also, a short-term position-memory (called optokinetic memory) has been found in the crab and the locust (Horridge 1966, a & b), and fly (Mastebroek 1982). These facts indicate many kinds of memory in insect's visual systems, but where they are, and how flies select these channels is completely unknown.

6-2-4. How to select the right channel.

The short-term motion memory depends on the prior motion state of a contrasting edge, the position of which is known to the motion-detection mechanism. So when perceiving an edge movement, the direction of motion is derived by comparison of this memory with the new location. Supposing, however, the edge was previously in motion. Then, the motion channels with the sigmoidal shaped response curve and the high-pass frequency characteristic would respond and transfer motion signals to the LFMSDs. On the other hand, if the edge was previously stationary, the channels with the bell-shaped response curve and the band-pass frequency characteristic are selected. Apparently, the course of switching motion signals between channels is completed gradually, because the cells need a certain period to adapt to the stimulus movement.

Switching motion signals into appropriate channels also can be implemented by using supra/sub-threshold mechanism (Foster 1971; Grzywacz & Koch 1987). It is proposed that, after the EMDs response to movement, all motion signals are sent to switch-cells via temporal filters. Therefore, sudden object movement from the steady state will generate relatively larger supra-threshold responses, which are switched into the band-pass channels, and meanwhile the other channels are still in the off state so that the band-pass channels characterize the responses of the LFMDs. But when facing continuous movement the response strength falls below the threshold because of the adaptation or temporal filtering, and the band-pass channel becomes inactive. All motion signals are then routed to the high-pass velocity channels, and the response is dominated by the high-pass channels.

The same effect can be achieved in another way, by non-linear lateral interactions between two kinds of motion channels. When a target starts to

move, the response component via the band-pass velocity channels is more active and strongly inhibits the others, thus the responses of the LFMDs are dominated by the characteristics of the band-pass channels. But after a certain period of time, the response components in the band-pass channels decline, and are inhibited by the response components from the high-pass velocity channels, now getting stronger, and as a result the LFMD behaviour is gradually characterized by the high-pass channels.

The bell-shaped and sigmoid response curves can also be explained as a result of nonlinear lateral interactions working at two different states. When responding to the movement of an object without prior-motion, only those EMDs that are directly facing the edge at the moment of starting the movement are excited at all, and no inhibition is coming from the adjacent units. Meanwhile the excited ones produce a stronger inhibition then those excited later, if the strength of the inhibition is proportional to the response of the preceding EMDs. As a result, the LFMSDs response is a bellshaped curve while the target is passing those EMDs. But when dealing with an object with continued movement, all the EMDs are at the same position relative to the stimulus and excited simultaneously, with similar response sensitivities and lateral interactions. Thus the LFMDs responses will never drop down while the object moves across those regions, and they therefore exhibit sigmoidal-shaped curves. As yet there is no direct proof of any particular mechanism to choose the motion channels, because the topic has hardly been considered previously.

To sum up, there may be two kinds of motion-detection channels for continuous movements or sudden movements, just as neurons can be divided into two groups - transient cells and sustaining cells. For avoidance of obstacles, the bell-shaped channels deal with velocity changes, with a fast and sensitive response.

Responses, which need accurate velocity tuning, can be only satisfied with the sigmoidal-shaped response curves provided by the high-pass channels.

6-3. What the cells H1 and V2 measure

6-3-1. Motion measurements of large-field motion-detectors.

What the H1 and V2 cells measure in response to movement is a primary challenge which has puzzled many researchers for decades. It is also essential to understand precisely how the visual system works, before the knowledge can be applied to other areas of research, such as machine vision.

Let us make a brief review of previous conclusions. Any movement, in direction and speed, can be detected by a symmetric network with directional lateral nonlinear interactions such as a threshold, clipping, multiplication, comparison, division or rectification, with convergence of at least two neighbouring receptor signals. Accordingly, several motion-detection models have been proposed, based on different lateral interactions, including the gradient scheme (Limb & Murphy, 1975: Ullman, 1981; and Marr & Ullman, 1981), the auto-correlation scheme (Hassenstein, Reichardt, 1951 - 1967; Poggio & Reichardt, 1973b; Kirschfeld, 1972 and Buchner, 1976), and logical null detector (Barlow & Levick, 1965), and a very simplified template model (Horridge, 1990). The measurements made by these models are significantly different, according to their mathematics. The auto-correlation model measures the contrast frequency of the stimulation by multiplying the outputs of the two contiguous neuro/photo-receptors. Similarly, the Barlow-Levick model just produces a response to some speeds of movement of an edge, by a asymmetrical lateral inhibition. The gradient model measures velocity of the movement by a division of local temporal and spatial derivatives (Jin & Srinivasan 1990). The template model

responds to the edge movements irrespective of their velocity and acceleration, by using a logical comparison as they pass by. Several of the possible models measure contrast frequency irrespective of pattern because they are driven by the number of edges passing a given point per second.

All four theories have enjoyed some success in explanation of certain aspects of the motion-detector responses, and in predictions of some visual behaviour. Differences in these predictions are at least a hint that each of these models is not complete, or is limited in interpreting the mechanisms of motion perception. For example, the multiplication model predicts that the response strength depends on the square of the contrast of light intensity, but there is no direct evidence so far proving that. It is argued that waveforms of characteristic movement response can be explained by multiplicative inputs from the lamina and medullary cells to movement detectors in the fly (DeVoe 1980). In the gradient model, any random noise which temporally changes the light intensity, generates a large response which significantly distorts the output. Anyway, it is clear that none of these models is sufficient to explain all of insect visual behaviour and nobody has yet succeded in making a complete artificial visual system using one of these models.

Theoretically, the ability of the nervous system to make measurements is severely limited by its signal transformation characteristics. All neurons are extremely limited in their information-carrying capacity. For H1 and V2 neurons, the signaling ability has a limit of around 300 spike/s in our experiments. Apparently, the cells are not capable of adequately measuring the motion increments-ranging from 0 °/s to over 300 °/s, even in steps of one per spike corresponding to one °/s increase, because of the noise, or variance in spike rate. This is a clear indication that the LFMDs do not treat the movement velocity as their main measurement, simply because in nature objects move in a

continuous speed range wider than that. Also it is doubtful that the cells measure the velocity, the contrast frequency or the spatial frequency if the speed is constant because they adapt to it. It is unlikely that flying animals can discriminate innumerable random velocities and spatial frequencies in distributed natural scenes, because the response to velocity depends on spatial frequency. We do not want to dismiss the possibility of interactions between the inter-neurons, making possible measurements of spatial frequency within a certain range, but the LFMD's adapt to any movement at a constant speed. It is unlikely that there are plenty of channels capable of responding to the different spatial frequencies, and neither velocity nor contrast frequency nor spatial frequency are of interest to the LFMDs because they adapt.

Therefore, in the face of these restrictions in signal transmission, it is not surprising that the cells should adopt some mechanism which can sufficiently encode some aspect of the stimulus over a wide range of speeds and various spatial structures, and being able to eliminate interference from various sources of noise, as well as change in ambient light intensity, and finally capable of keeping some constant measurements throughout the processing, so that all associated cells have the same response-coordinates. Our results in fact demonstrate that the cells do measure velocity contrast irrespective of the other parameters (Chapter 5).

6-3-2. Velocity contrast measurement

There are several lines of evidence indicating that the large field motion-sensitive neurons measure velocity contrast. Theoretically, the abstraction of velocity contrast is the only measure that can satisfy two conditions, a) enabling the cells to use their firing capability fully and b) to encode any movements efficiently, irrespective of any random noise. Some phenomena, found in the

LFMDs, such as adaptation, the gain control and lateral interaction, also hint that velocity contrast and its direction are the only parameters of interest to the visual system.

That the LFMDs respond to velocity contrast irrespective of contrast frequency, spatial frequency etc, gets strong support from the appearance of a gain control mechanism in the responses. It is known that one purpose of the gain control is to adjust the strength of the response to enhance the relative sensitivity to changes in strong stimuli. The adaptation of the cells response to continuous movement, which has been widely studied (Zaagman et al. 1983; and Maddess 1985), provides powerful evidence for the existence of gain control. The function of adaptation is to reduce the gain to protect the system from saturation, so retaining its sensitivity to changes.

The conclusion has further support from the finding that there is a strong lateral interaction between the inter-neurons which send motion signals to the LFMDs. This dominates the LFMD's responses and probably leads to the measure of velocity contrast. Lateral interaction is a common feature of many aspects of visual function, already discussed in anatomical and functional terms by many authors. For example, one role of lateral interaction is to suppress the low-spatial-frequency components of the visual scene as well as to block out the low-temporal-frequency components of the visual flow, filtering out signals which are of little use in detecting movement (Srinivasan and Dvorak 1980). The most significant role of lateral interaction is primarily to emphasize the changes in the inputs, and ultimately to enhance contrasts. Of course, which contrast is enhanced in the system depends on how the system's components respond. Considering a system which is composed of many parallel distributed elementary units with lateral inhibition, if each element is locally sensitive to velocity, the whole system will most likely abstract velocity contrast. The LFMDs are just this

kind of system. In fact, the possibility of lateral interaction in the LFMDs inputs has already been discussed in previous sections; the best evidence came from the appearance of the inhibitory phenomenon at the moment of changing the velocity. With the stimulus of a black bar briefly jumping in the preferred direction with prior-motion, strong excitation and inhibition phases corresponding to the velocity increment and decrement appear at the moment of jumping in the response of the H1 and V2 neurons and follow the Mach pattern. An example recorded from V2 is shown in Fig.4-15. The Mach band, of course, is a typical product of lateral inhibition. So if we agree that the LFMD's is just a system consisting of many parallel distributed EMDs each of which is sensitive to edge motion with lateral interaction by neighbouring units, the response of the whole system must relate to velocity contrast measurements.

Support also comes from the fact that many kinds of neurons appear to be interested in encoding stimulus contrasts. A typical example is the photoreceptor cell in the processing of light intensity. In nature, the light intensities vary over a range of seven log units; by contrast, the range of the photoreceptor cells is only over three log units. Obviously, it is a headache for the cells to measure so wide a range of light intensity with so limited a response ability. However, the cells are capable of compressing the seven log units of light intensity into the gain variation of about three. The solution, suggested by Norman & Werblin (1974) and Laughlin (1981), is to use the photometric contrast as the encoded parameter. Our previous experiment, on the photoreceptor cells of the locust stimulated by light, in which the intensity was sinusoidally modulated, also reveals that the response contrast is nearly linearly dependent on the intensity contrast irrespective of the mean intensity. Apparently, all of the above facts are a indication that from the first stage of processing information, the cells start to encode contrast. Subsequent cells adapt in a similar way, to enable them to use their limited response range to deal with a wider range of signals. So, it is

possible that the visual system encodes contrast of various kinds at various stages from the beginning to the end of the information transfer.

The ratio of the response contrast of the H1 and V2 to the velocity contrast of the stimulus keeps a constant value of approximately 0.60 ± 0.09 in the transient response irrespective of the changes in velocity (Fig.4-13b). Here, the response contrast is measured by dividing the peak transient firing frequency of the cells to the bar jump by the mean firing frequency at the level of responding to prior-motion; the velocity contrast is measured by dividing the speed of jump by the speed of the prior-motion. This golden ratio, representing a relationship between the initial inputs and the eventual outputs, not only reveals what is the most significant signal the LFMD's should extract primarily - that is velocity contrast, but also tells how the cells respond to it - taking a constant ratio of 0.62 to the stimulus contrast. This ratio may be a common and practical rule serving all kinds of information processings, and perhaps other cells use it to deal with signals efficiently - without loosing and wasting, because any measure can be divided proportionally at this constant factor stage by stage for ever without distortion or disturbance; and the signals which are of little or no use in determining ultimate responses are reduced.

Finally, the most critical support comes from the whole experiment of chapter five with sinusoidally-modulated moving sine-wave grating, the neuron measures velocity modulation with velocity contrast from 0.1 to 1.0 and modulation frequency up to 12 Hz, irrespective of contrast frequency, mean velocity, acceleration, and velocity modulation frequency in the steady response state. This result shows that the H1 neuron mainly abstracts the velocity modulation of the object movement from various other parameters.

The motion detection system works as a special kind of coordinate conversion. At the first stage, the EMDs transform all objects, which obviously are distributed in a real natural light-illuminance space, into a correspondent motion domain, which only displays the motion and direction - telling how big the speed is at a certain spatial position. Then, the 'objects' are converted further into a velocity contrast domain by the nerve-network, which is able to tell the positions and directions of the velocity changes. Now, we can clearly see the advantage of contrast measurement. By measuring velocity contrast, the unit motion detectors can concentrate their limited response ability to deal efficiently with the most useful signals - detecting the edges of moving objects, which can serve almost all aspects of the animal's visual responses. The reason is clear by considering a simple case. Supposing that a fly looks at a moving object against a relatively slower background. In the velocity contrast space, only those places where the edges of the moving object are located are significant, which means only around these places with motion contrast. In the other places, the velocity contrasts are simply equal to 0. Eventually, an object is only a closed circle at a certain place in the velocity contrast space. This measure, of course, enables the cells to reconstruct the outline of a moving object efficiently using just a few signals, but only for a moving object, and they cannot see a stationary object, an object in a picture, or a shadow on the ground.

REFERENCES

Arnett, D.W. 1971 Receptive field organization of units in the first optic ganglion of Diptera. Science 173, 929-923.

Arnett, D.W. 1972 Spatial and temporal integration properties in first optic ganglion of Dipterans. J. Neurophysiol. Vol. 35(4), 429-444.

Baker, C.L. and Braddick,O.J. 1985 Temporal properties of the short-range process in apparent motion. Motion perception 14(2), 181-192.

Barlow, H.B. and Levick, W. R. 1965 The mechanism of directionally selective units in rabbit's retina. J. Physiol. 178:477-504

Bishop, C.A. and Bishop, L.G. 1981 Vertical motion detectors and their synaptic relations in the third optic lobe of the fly. J. Neurobiol. 12(3), 281-296.

Bishop, L.G. and Keehn, D.G. 1966 Two types of neuron sensitive to motion in the optic lobe of the fly. Nature 212, 1374-1376.

Borst, A. and Egelhaff, M. 1987 Temporal modulation of luminance adapts time constant of fly movement detectors. Biol. Cybern. 56, 209-215.

Borst, A., Egelhaaf, M., Reichardt, W. 1989 The nonlinear mechanism of direction selectivity in the fly motion detection system. Naturwissenschaften, 76, 32-35.

Borst, A., Egelhaaf, M. 1989 Principles of visual motion detection. TINS, Vol. 12 No. 8 297-306.

Buchner, E. 1976 Elementary movement detectors in an insect visual system. Biol. Cybern., 23, 157-160.

Buchner, E. Buchner, S. and Hengstenberg, R. 1979 2-Deoxy-D-glucose maps movement-specific nervous activity in the second visual ganglion of Drosophila. Science. 205(4407), 687-688.

Buchner, E. 1984 Behavioural analysis of spatial vision in insect. In Ali MA (ed) Photoreception and vision in invertebrates. Plenum Press, New York London. 561-621.

Bulthoff, E. and Gotz, K.G. 1979 Analogous motion illusion in man and fly. Nature. Apr 12, 278(5705), 636-638.

Burtt, E.T. and Catton, W.T. 1954 Visual perception of movement in the locust. J. Physiol. 125, 566-580.

Collett, T.S. and Blest, A.D. 1966 Binocular, directionally selective neurones, possibly involved in the optomotor response of insects. Nature 212, 1330-1333.

Collett, T.S. 1980 Angular tracking and the optomotor response and analysis of visual reflex interaction in a hoverfly. J. Comp Physiol A

David, C.T. 1982 Compensation for height in the control of groundspeed by Drosophila in a new 'Barber's Pole' wind tunnel. J. Comp. Physiol. 147, 485-493.

de Ruyter van Steveninck, R.R. Zaagman, W.J. and Masterbroek, H.A.K. 1986 Adaptation of transient responses of a movement-sensitive neuron in the visual system of the blowfly Calliphora erythrocephala. Biol. Cybern. 54, 223-236.

DeVoe, R.D. and Ockleford, E. M. 1976 Intracelluar response from cells of the medulla of the fly, Calliphora erythrocephala. Biol. Cybern. 23, 13-24

DeVoe, R.D. 1980 Movement sensitivities of cells in the fly's medulla. J. Comp. Physiol. 138, 93-119

DeVoe, R.D., Kaiser, W., Ohm, J. and Stone, L.S. 1982 Horizontal movement detectors of honeybees: Directionall-selective visual neurons in the lobula and brain. J. Comp. Physiol. 147, 155-170.

Dvorak, D.R., Bishop, L.G. and Eckert, H.E. 1975 On the identification of movement detectors. J. Comp Phys. 100, 5-23.

Dvorak, R.D., Srinivasan, M.V. and French, A.S. 1979 The waterfall illusion in an insect visual system. Vision. Res. 19(12), 1435-1437.

Dvorak, D.R., Srinivasan, M.V. and French, A.S. 1980 The contrast sensitivity of fly movement-detecting neurons. Vision Res. 20, 397-407.

Eckert, H. 1980 Response properties of the H1 neuron in the third optic ganglion of the blowfly, Phaenicia. J. Comp Physiol. 135, 29-39.

Eckert, H. and Meller K. 1981 Synaptic structures of identified motion sensitive neurons in the brain of the fly, Phaenicia. Verh Dtsch Zool Ges. 179.

Eckert, H. 1981 The horizontal cells in the lobula plate of the blowfly, Phaenicia sericata. J. Comp Physiol. 143, 511-526

Eckert, H. and Hamdorf, K. 1981 Action potentials in "Non-spiking" visual interneurons. Z. Naturforsch 36c, 470-474.

Eckert, H. and Hamdorf, K. 1981 The contrast frequency-depenence: A criterion for judging the Non-participation of neurones in the control of behavioural responses. J. Comp. Physiol. 145, 241-247

Eckert, H. 1982 The vertical-horizontal neurone (VH) in the lobula plate of the blowfly, Phaenicia. J. Comp Physiol. 149, 195-205

Egelhaaf, M. 1985a On the neuronal basis of figure-ground discrimination by relative motion in the visual system of the fly. Part 1. Behavioural constraints imposed on the neuronal network and the role of the optomotor system. Biol. Cybern. 52, 123-140.

Egelhaaf, M. 1985b On the neuronal basis of figure-ground discrimination by relative motion in the visual system of the fly. Part 2. Figure-detection cells, a new class of visual interneurons. Biol. Cybern. 52, 195-209.

Egelhaaf, M. 1985c On the neuronal basis of figure-ground discrimination by relative motion in the visual system of the fly. Part 3. Possible input circuitries and behavioural significance of the FD-cells. Biol. Cybern. 52, 267-280.

Egelhaaf, M. and Reichardt, W. 1987 Dynamic response properties of movement detectors: theoretical analysis and electrophysiological investigation in the visual system of the fly. Biol. Cybern. 56:69-87

Egelhaaf, M., Hausen, K., Reichardt, W. and Wehrhahn, C. 1988 Visual sense control in flies relies on neuronal computation of object and background motion. Trends. Neurosi. 11(8), 351-358.

Egelhaaf, M., Borst, A. and Reichardt, W. 1989 Computuational structure of a biological motion-detection system as revealed by local detector analysis in the fly's nervous system. J. Optical Soc. America. A. 6(7): 1070-1087

Egelhaaf, M. and Borst, A. 1989 Transient and steady-state response properties of movement detectors. J. Optical Soc. America A. 6: 116-127

Emerson, R.C., Citron, M.C., Vanghn, W.J. and Klein, S.A. 1987 Nonlinear directionally selective subunits in complex cells of cat striate cortex. J. Neurophysiol. 58(1), 33-65.

Fennema, E.V. and Thompson, W.B. 1979 Velocity determination in scenes containing several moving objects. Computer graphics and image processing. 9, 301-315.

Foster, D. 1971 The response of the human visual system to moving spatially-periodic patterns: further analysis. Vision Res. 11, 57-81.

Foster, D.H. 1971 A model of human visual system in its response to certain classes of moving stimuli. Kybernetik. 8, 69-84.

Franceschini, N. 1975 Sampling of the visual environment by the compound eye of the fly: Fundamentals and applications. In: Snyder A.W. and Menzel, R. (eds) Photoreceptor optics. Springer, Berlin Heidelberg New York, pp 98-125.

Franceschini, N. 1985 Early processing of colour and motion in a mosaic visual system. Neurosci. Res. Suppl. 2, 517-549.

Franceschini, N., Riehle, A. and Le Nestour, A. 1989 Directionally-selective motion detection by insect neurons. In: Facets of Vision, (eds. D. Stavenga and R. Hardie), pp 360-390, Berlin: Springer-Verlag.

Geiger, G. 1975 "Short-term learning" in flies. Naturwissenschaften. 62.

Grzywacz, N.M., and Koch, C. 1987 Functional properties of models for direction selectivity in the retina. Synapse. 1(5), 417-434.

Gotz, K.G. 1965 Die optischen Ubertragungseigenschaften der Komplexaugen von Drosophila. Kybernetik. 2,215-221.

Gotz, K.G. 1968 Flight control in Drosophila by visual perception of motion. Kybernetik. 4(6), 199-208.

Gotz, K.G. 1972 Processing of cues from the moving environment in the Drosophila navigation system. In: Information processing in the visual system of Arthropods, ed. by R. Wehner, pp 255-263. Berlin-Heidelberg-New York : Springer.

Gotz, K.G. 1975 The optomotor equilibrium of the Drosophila navigation system. J. Comp. Physiol. 90, 187-210.

Gotz, K.G. Buchner, E. and Straub, C. 1978 Elementary detectors for vertical movement in the visual system of Drosophila. Biol. Cybern. 31(4), 234-242.

Gotz, K.G. and Buchner, E. 1978 Evidence for one-way movement detection in the visual system of Drosophila. Biol. Cybern. 31(4), 243-248.

Gotz, K.G. Bulthoff, H. 1979 Analogous motion illusion in man and fly. Nature. 278(5705), 636-638.

Gotz, K.G., Hengstenberg, B. and Biesinger, R. 1979 Optomotor control of wing beat and body posture in Drosophila. Biol. Cybernetics. 35, 101-112.

Gould, J.L. 1985 How bees remember flower shapes. Science 227, 1492-1494.

Gould, J.L. 1986 Pattern learning by honey bees. Ainm. Behav. 34, 990-997.

Gould, J.L. 1987 Landmark learning by Honey bees. Anim. Behav. 35, 26-37.

Gould, J.L. 1987 Honey bees store learned Flower-landing behaviour according to time of day. Anim. Behav. 35, 1579-1581.

Hassenstein, B. 1951 Ommatidienraster und afferente Bewegungs-Integration. Z. vergl. Physiol. 33, 301-326.

Hassenstein, B. and Reichardt, W. 1953, Z. Naturforschg. 8b, 518.

Hassenstein, B. and Reichardt, W. 1956 System-theoretische Analyse der Zeit-Reihenfolgenund Vorzeichenauswertung bei der Bewegungsperzeption des Russelkafers Chlorophanus. Z. Naturforsch. 11b, 513-524.

Hassenstein, B. and Reichardt, W. 1956 Functional structure of a mechanism of perception of optic movement. Proceeding of the first International Congress on Cybernetics, Namur 797.

Hassenstein, B. 1959 A cross correlation process in the nervous center of an insect eye. Nuovo. Cimento. X.13, 617-619.

Hassenstein, B. 1967 On physiologic data processing with respect to human cortex vision. Naturwissenschafften. 54(12), 321-322.

Hateren JH van., and Caughlin, S. B. 1990 Directional tuning curves, elementary movement detectors, and the estimation of the direction of visual movement. Vision. Res. 30(4), 603-614.

Hausen, K. 1976a Strukture, Funktion und Konnektivitat bewegungsempfindlicher Interneuronen im drittrn optischen Neuropil der Schmeibfliege Calliphora erythrocephala. Diss. Univ. Tubingen.

Hausen, K. 1976b Functional characterization and anatomical identification of motion sensitive neurons n the lobula plate of blowfly. Z. Naturf. 31c, 629-633.

Hausen, K. 1976c Functional structure and connectiveity of motion-sensitive interneurons in the lobula plate of Diptera. Verh Dtsch. Zool. Ges. 254

Hausen, K. 1981 Monocular and binocular computation of motion in the lobula plate of the fly. Verh. Dtsch. Zool. Ges. 49-70.

Hausen, K. 1982a Motion sensitive interneurons in the optomotor system of the fly. I. The horizontal cells: structure and signals. Biol. Cybern. 45: 143-156

Hausen, K. 1982b Motion sensitive interneurons in the optomotor system of the fly. II. The horizontal cells: receptive field organization and response characteristics. Biol. Cybern. 46: 67-79

Hausen, K. Wehrhahn, C. 1983 Microsurgical lesion of horizontal cells changes optomotor yaw responses in the blowfly calliphora. Proc. R. Soc. London B. 219, 211-216.

Hausen, K. 1984 The lobula-complex of the fly: structure, function and significance in visual behaviour . In Ali MA (ed) Photoreception and vision in invertebrates. Plenum. New York. pp 523-559

Hausen, K. and Egelhaaf, M. 1989 Neural mechanisms of visual course control in insects. In: Facets of Vision. (Stavenga, D. G. and Hardie, R. C. eds.) Springer-Verlag. New York pp 391-424

Hausen, K. and Wehrhahn, C. 1990 Neural circuits mediating visual flight control in flies, prat 2. separation of two control systems by microsurgical brain lesions. J. Neurosci. 10(1), 351-360.

Hengstenberg, R., Hausen, K. and Hengstenberg, B. 1982 The number and structure of giant vertical (VS) cells in the lobular plate of the blowfly Calliphora erythrocephala. J. Comp. Physiol. 149, 163-177.

Hengstenberg, R. 1982 Common visual response properties of giant vertical cells in the lobula plate of blowfly Calliphora. J. Comp. Physiol. 149, 179-193.

Hengstenberg, R. 1989 Stabilizing head/eye movements in the blowfly Calliphora erythrocephala. IBRO Symposium. Head/Neck System, Fontainbleau, 1989.

Hertel, H. and Maronde, U. 1987 The physiology and morphology of centrally projecting visual interneurons in the honeybee brain. J. Comp. Biol. 133, 301-315.

Hildreth, E.C. and Koch, C. 1987 The analysis of visual motion: from computational theory to neuronal mechanisms. Annu. Rev. Neurosci. 10, 477-533.

Horn, E. and Wehner, R. 1975 The mechanism of visual pattern fixation in the walking fly, Drosophila melanogaster. J. Comp. Physiol. 101, 39-56.

Horridge G.A., Scholes, J. H., Shaw, S. and Tunstall, J. 1965 Extracellular recordings from single neurons in the optic lobe and brain of the locust. In: The physiology of the insect central nervous system. (Treherne, J. E. and Beament, J. W. L. eds.) London and New York. The Academic Press.

Horridge, G.A. 1966a Optokinetic memory in the crab, Carcinus. J. exp. Biol. 44:233-245

Horridge, G.A. 1966b Optokinetic memory in the locust. J. Exp. Biol. 44:255-261

Horridge, G.A.1990 A template theory to relate visual processing to digital circuitry. Proc. R. Soc. Lond. B 239:17-33

Horridge, G.A. 1990 Semivision: A Summary of the template theory of early visual processing. Phil. Trans. Roy. Soc. B.

Horridge, G.A. and Marcelja, L. 1990 Response of the H1 to contrast and moving bars. Phil. Trans. Roy. Soc. (in press)

Horridge, G.A. and Marcelja, L. 1991 Response of the H1 neuron to jumped edges. Phil. Trans. Roy. Soc. (in press)

Horridge, G.A. and Marcelja, L. 1991 unpublished data:

Hubel, D.H 1957 Tungsten microelectrode for recording from single units. Science. 125, 549-550.

Hubel, D.H. and Wiesel, T.N. 1962 Receptive fields, binocular interaction, and functional architecture in the cat's visual cortex. J. Physiol. 160, 106-154.

Ibboston, M. R. Goodman, L.J. 1990 Response characteristics of four wide-field motion-sensitive descending interneurons in Apis Mellifera. J. Exp. Biol. 148, 255-279.

Jin, Z.F. and Srinivasan, M.V. 1990 Gradient schemes for measuring image velocity. Visual Neuroscience. 5, 261-271.

Kaiser, W. and Bishop, L. 1970 Directionally selective motion detecting units in the optic lobe of the honeybee. Z. Vergl. Physiol. 67:403-413

Kien, J. 1974a Sensory integration in the locust optomotor system. I: behavioural analysis. Vision Res. 14:1245-1254

Kien, J. 1974b Sensory integration in the locust optomotor system. II: direction sensitive selective neurons in the circumoesophageal connectives and the optic lobe. Vision Res. 14: 1255-1268

Kien, J. 1975 Motion detection in locusts and grasshoppers. Oxford Symposium pp 410-422

Kien, J. 1975 Neuronal mechanisms subserving directional selectivity in the locust optomotor system. J. Comp. Physiol. 113, 161-179.

Kirschfeld, K. 1972 Optics of the compound eye: 1. The visual system of Musca: Studies on optics, structure and function. In: Information processing in the visual systems of Arthropods (Wehner, R. ed.) Springer- Verlag, New York. pp 61-74

Kunze, P. 1961 Untersuchung des Bewegunssehens fixiert fliegender Bienzen. Z. vergl. Physiol. 44: 656-684

Land, M.F. and Collett, T.S.1974 Chasing behaviour of houseflies (Fannia cannicularis). A description and analysis. J. Comp. Physiol. 89, 331-357.

Laughlin, S.B. 1981 Neural principles in the peripheral visual system of invertebrates. In: Handbook of Sensory Physiology, Vol. 7(6B), (H. Autrum, Ed.), pp 133-280. Berlin: Springer

Lee, D.N. 1980 The optic flow field: the foundation of vision. Phil. Trans. Soc. R. Soc. Lond. B290, 169-179.

Limb, J.O. and Murphy, J.A. 1975 Estimating the velocity of moving images in television signals. Computer Graphics and Imaging Processing. 4, 311-327.

Maddess, T. and Laughlin, S.B. 1985 Adaptation of the motion sensitivite neuron H1 is generated locally and governed by contrast frequency. Proc. R. Soc. Lond. B 225, 251-275.

Maddess, T. 1986 Afterimage-like effects in the motion-sensitive neuron H1. Proc. R. Soc. Lond. B 228, 433-459.

Marmarelis, P.Z. and McCann, G.D. 1973 Development and application of white-noise modeling techniques for studies of insect visual nervous system. Kybernetik. 12(2), 74-89.

Marr, D. and Ullman, S. 1981 Directional selectivity and its use in early visual processing. Proc. R. Soc. Lond. B. 211, 151-180.

Masterbroek, H.A.K. 1974 Stochastic structure of neural activity in the visual system of the blowfly. Thesis. Groningen University.

Mastebroek, H.A.K., Zaagman W.H., Lenting B.P,M. 1980 Movement detection: Performance of a wide-field element in the visual system of the blowfly. Vision Res. 20, 467-474.

Mastebroek,H.A.K., Zaagman W.H. and Lenting, B.P.M. 1982 Memory-like effects in fly vision: Spatio-temporal interactions in a wide-field neuron. Biol. Cybern. 43, 147-155.

McCann, G.D. and MacGinitie, G.F. 1965 Optomotor response studies of insect vision. Proc. R. Soc. Lond. 163, 369-401.

McCann, G.D. 1974 Nonlinear identification theory models for successive stages of visual nervous system of flies. J. Neurophysiol. 37, 869-895.

Menzel, R. and Erber, J. 1978 Learning and memory in bees. Sci. Ameri. 239, 102-110.

Menzel, R. 1983 Neurobiology of learning and memory: The honeybee as a model system. Naturwissenschaften 70, 504-511.

Menzel, R. 1985 Learning in honey bees in an ecological and behavioural context. In: Experimental Behavioural Ecology. (ed. Holldobler, D. and Lindauer, M.), pp. 55-74. Stuttgart: Fischer, G.

Merrill, E.G. and Ainsworth, A. 1972 Glass-coated platinum-plated tungsten microelectrodes. Med. Biol. Eng. 10(5), 662-672.

Nakayama, K. and Loomis, J.M. 1974 Optical velocity patterns, velocity-sensitive neurons, and space perception: A hypothesis. Perception 3(1), 63-80.

Norman, R.A. and Werblin, F.S. 1974 Control of retinal sensitivity. I. Light and dark adatation of vertebrate rods and cones. J. Gen. Physiol. 63, 37-61.

Oldberg, R.M. 1981 Object an self-movement detectors in the ventral nerve cord of the dragonfly. J. Comp. Physiol. 141, 327-334.

O'Shea, M., Rowell, C.H.F. and Williams, J.L.D. 1977 The neuronal basis of a sensory analyser, the acridid movement detector system. IV. The preference for small field stimuli. J. Exp. Biol. 68, 157-185.

Osorio, D. 1986 Directionally selective cells in the locust medulla. J. Comp. Physiol. 159, 841-847.

Osorio, D, 1987 The temporal properties of non-linear transient cells in the locust medulla. J. Comp. Physiol. 161, 431-440.

Osorio, D. 1987 Temporal and spatial properties of sustaining cells in the medulla of the locust. J. Comp. Physiol. 161, 441-445.

Pick, B. 1976 Visual pattern discrimination as an element of the fly's orientation behaviour. Biol. Cybern. 23, 171-180.

Pick, B. and Buchner, E. 1979 Visual movement detection under light- and dark-adaptation in the fly, Musca domestica. J. Comp. Physiol. 134, 45-54.

Pinter, R.B. Osorio, D. and Srinivasan, M.V. 1990 Matched filtering in the visual system of the fly: Large monopolar cells of the lamina are optimized to detect moving edges and blobs. Proc. R. Soc. Lond. B 240, 279-293.

Poggio, T. and Reichardt, W. 1973 Considerations on models of movement detection. Kybernetik 13: 223-227

Poggio, T. and Reichardt, W. 1976 Visual control of orientation behaviour in the fly. Toward the underlying neural interactions Q. Rev. Biophys. 9, 377-438.

Prazdny, K. 1980 Egomotion and relative depth map from optic flow. Biol. Cybern. 36, 87-102.

Reichardt, W. 1957 Autokorrelationsauswertung als Funktionsprinzip des Zentralnervensystems. Z. Naturforschg. 12B, 447.

Reichardt, W. 1961 Uber das optische Auflosungsvermogen der Facettenaugen von Limulus. Kyberntik 1, 57.

Reichardt, W. 1961 Autocorrelation , a principle for evaluation of sensory information by the central nervous system . In Rosenblith W. A. (ed) Principles of sensory communication. Wiley. New York. pp 303-317

Reichardt, W. 1969 Transduction and processing of optical data. In The neurosciences: second study programme. Schmitt, F. O. ed. Rockfeller Univ. Press. New York pp 494-511

Reichardt, W. 1973 Musterinduzierte flugorientierung. Verhaltensversuche an der Fliege Musca domestica. Naturwissenschaften 60, 122-138.

Reichardt, W. and Poggio, T. 1976 Visual control of orientation behaviour in the fly.Part I. A quantitative analysis. Q. Rev. Biophys. 9:311-375

Reichardt, W. and Poggio, T. 1979 Figure-ground discrimination by relative movement in the visual system of the fly. Biol. Cybern. 35, 81-100

Reichardt, W. and Guo, A. K. 1986 Elementary pattern discrimination. Biol Cybern. 53, 285-306

Reichardt, W. 1987 Evaluation of optical motion information by movement detectors. J. Comp. Physiol. 161, 533-547.

Reichardt, W. and Egelhaaf, M. 1988 Properties of individual movement detectors as derived from behavioural experiments on the visual system of the fly. Biol. Cybern. 58, 287-294

Rind, F.C. 1983 A directionally sensitive motion detecting neuron in the brain of a moth. J. Exp. Biol. 102, 253-271.

Rind, F.C. 1987 Non-directional movement sensitive neurons of the locust optic lobe. J. Comp. Phsiol. A 161(3), 477-494.

Schouten, J.F. 1967 Subjective stroboscopy and a model of visual movement detectors. In: Wathen-Dum, W. (ed) Models for the perception of speech and visual form. MIT Presss, Cambridge MA, pp 44-55.

Schuling, F.H. Mastebroek, H.A.K., and Lenting, B.P.M. 1989 Properties of elementary movement detectors in the fly Calliphora erythrocephala. J. Comp. Physiol. 165, 179-192.

Sobey, P. and Horridge, G.A. 1990 Simulation of the template model of vision. Proc. R. Soc. Lond. B 240, 211-229.

Srinivasan, M.V. and Bernard, G.D. 1976 A proposed mechanism for multiplication of neural signals. Biol. Cybern. 21, 227-236.

Srinivasan, M.V. 1977 A visually-evoked roll response in the housefly. J. Comp. Physiol. 119, 1-14.

Srinivasan, M.V. and Bernard, G.D. 1977 The pursuit response of the housefly and its interaction with the optomotor response. J. Comp. Physiol. 115, 101-117.

Srinivasan, M.V. and Dvorak, D.R. 1980 Spatial processing of visual information in the movement-detecting pathway of the fly. Characteristics and functional significance. J. Comp. Physiol. 140, 1-23.

Srinivasan, M.V. Laughlin, S.B., and Dubs, A. 1982 Predictive coding: a fresh view of inhibition in the retina. Proc. R. Soc. Lond. B216, 427-459.

Srinivasan, M.V. 1983 The impulse response of a movement-detecting neuron and its interpretation. Vison Res. 23, 659-663.

Strausfeld, N.J. 1984 Functional neuroanatomy of the blowfly's visual system. In: Photoreception and vision in Invertebrates. (Ali, M.A. ed.) pp 483-522, NATO ASI Series Plenum Press, New York

Tinbergen, J. 1987 Photoreceptor metabolism and visually guided landing behaviour of flies. Thesis, University of Groningen.

Thorson, J. 1966 Small-signal analysis of a visual reflex in the locust. I. Input parameters. Kybernetik 3, 4-52.

Thorson, J. 1966 Small-signal analysis of a visual reflex in the locust. II. Frequency dependence. Kybernetik 3, 53-66.

Torre, V. and Poggio, T. 1978 A synaptic mechanism possibly underlying directional selectivity to motion. Proc. R. Soc. Lond. B 202, 409-416.

Ullman, S. 1981 Analysis of visual motion by biological and computer system. IEEE Computer 14, 57-69.;

Umeda, K. and Tateda, H. 1985 Visual interneurons in the lobula complex of Boettcherisca. J. Comp. Physiol. A 157, 831-836.

van Doorn, A.J. and Koenderink, J.J. 1976 A directionally sensitive network. Biol. Cybern. 21, 161-170.

van Doorn, A.J. and Koenderink, J.J. 1982a Temporal properties of the visual detectability of moving spatial white noise. Exp. Brain Res. 45, 179-188.

van Doorn, A.J. and Koenderink, J.J. 1982b Spatial properties of the visual detectability of moving spatial white noise. Exp. Brain Res. 45, 189-195.

van Hateren, J.H.1987 Photoreceptor optics and neural microcircuitry in insect eye. Thesis, University of Groningen

van Hateren, J.H.1987 Neural superposition and oscillations in the eye of the blowfly. J. Comp. Physiol. A 161, 849-855.

van Hateren, J.H. 1990 Directional tuning curves, elementary movement detectors, and the estimation of the direction of visual movement. Vision. Res. 30(4), 603-614.

van Hateren, J.H. Srinivasan, M.V. and Wait, P.B. 1990 Pattern recognition in bees: Orientation discrimination. J. Comp. Physiol. (in press)

van Santen, J.P.H. and Sperling, G. 1984 Temporal covariance model of human motion perception. J. Opt. Soc. Am. A 1, 451-473.

van Santen, J.P.H. and Sperling, G. 1985 Elaborated Reichardt detectors. J. Opt. Soc. Am. A 2, 300-321.

Wagner, H. 1982 Flow-field variables trigger landing in flies. Nature 297, 147-148.

Wehner, R, 1981 Spatial vision in arthropods. In: Handbook of sensory physiology. VII/c (ed. Autrum, H.J.), pp. 287-616. Berlin, Heidelberg and New York: Springer Verlag.

Wilson, M. 1978 The functional organisation of locust ocelli. J. Comp. Physiol. 124, 297-316.

Wilson, H.R. 1985 A model for direction selectivety in threshold motion perception. Biol. Cyber. 51, 213-222.

Wolf, R. and Heisenberg, M. 1980 On the fine structure of yaw torque in visual flight orietation of Drosophila melanogaster. II. A temporally and spatially variable weighting function for the visual field (visual attention). J. Comp. Physiol. 140, 69-80.

Zaagman, W,H., Mastebroek, H,A,K., Buyse, T., and Kuiper, J.W. 1977 Receptive field characteristics of a directionally selective movement detector in the visual system of the blowfly. J. Comp. Physiol. 116, 39-50.

Zaagman, W.H., Mastebroek, H.A.K., and Kuiper, J.W. 1978 On the correlation model: performance of a movement detecting neural element in the fly visual system. Biol. Cybern. 31, 163-168.

Zaagman, W.H., Mastebroek, H.A.K., and De Ruyter van Steveninck, R. 1983 Adaptive strategies in fly vision: On their image-processing qualities. IEEE Trans. SMC 13, 900-906.